NOTE ON THE NEGATIVE REACTION UNDER LIGHT-ADAPTATION IN THE PLANARIAN

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One figure

It has been shown[1] that the planarian tends to become active under the influence of light and to come to rest in the shadow or dark,[2] a form of behavior that results most generally in bringing the animal into regions distant from the source of light. It has also been shown [3] that photic stimulation elicits a negative response; that is to say, the animal tends to turn from the source of light. This response is due, however, not to the direction of the rays of light as such, but to a tendency on the part of the animal to turn from the side of more intense illumination. A planarian will move along a narrow strip of shadow directly toward the source of light, if in so doing it avoids the areas of more intense illumination on either side of the strip.[4] The turning from the light in directive illumination has thus been explained as a negative response to a difference of intensity of light upon the two sides; in other words, the creature, being more strongly illuminated on the side toward the light than on the side away from the light, gives the negative reaction away from the light source. In explanation of this response Loeb [5] has applied the term *Unterschiedsempfindlichkeit*, as opposed to a heliotropism under which the animal responds to the direction of the light, independent of its intensity; and the most generally accepted explanation appears to be some form of differential sensitivity. This view seems, however, to have been accepted less upon positive experimental evidence than because of the inadequacy of the other theories.

[1] Loeb, J. *Arch. f. d. ges. Physiol., 54*, 1893, p. 101; *56*, 1894, p. 255.

[2] This form of behavior has been called *negative photopathy* by Washburn, *Animal Mind*, 1908, pp. 167ff.; *photokinesis* by Englemann, *Arch. f. d. ges. Physiol., 30*, 1883, pp. 107ff. Walter later applied the term *photokinesis* to the behavior of planarians, *Jour. Exper. Zool., 5*, 1907, p. 49.

[3] Parker and Burnett. *Am. Jour. Physiol., 4*, 1900, pp. 373ff.

[4] Cole, L. J. *Jour. Comp. Neur. and Psych., 17*, 1907, p. 193.

[5] *Arch. f. d. ges. Physiol., 54*, 1893, p. 101.

In the course of experiments upon the modification of behavior in the flat-worm, the writer believes that he has observed behavior that argues directly in favor of a differential sensitivity; and it is the purpose of this note to describe the observations.

MATERIAL

The subjects used were specimens obtained from a stream near Ithaca, New York, and were partially identified as *Planaria torva*, although the identification was not absolutely positive.
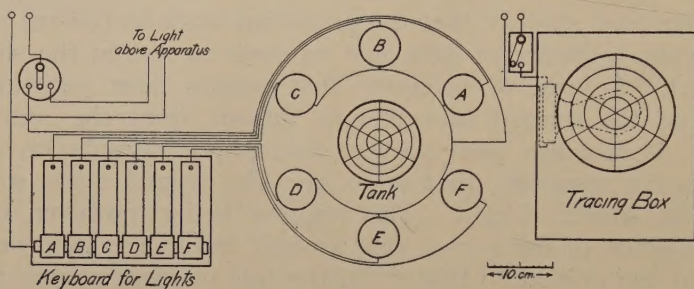
APPARATUS

The apparatus was set up in a dark room. The essential features consisted of a circular glass tank, for which a crystallization dish was used, 12.5 cm. in diameter by 6 cm. high, and six 16 cp. electric lights (A, B, C, D, E, and F in the figure), arranged in a circle about the tank, 15 cm. from its center, and set at such a height that the centers of the bulbs were about 1 cm. above the level of the bottom of the tank. The lights were so arranged that they could be individually thrown in or out of circuit. They were controlled from a keyboard, which was constructed of strips of tin. The strips were insulated at the points of contact with the fingers, and so placed above a metal rod, that each strip, when pressed down, completed the circuit for a single lamp. One meter above the center of the tank was suspended a single 16 cp. light. This light and the system of lights below were controlled by a double-throw switch, in such a way that when the lower lights were in use the upper could not be, and *vice versa*. The tank was placed upon a sheet of paper, ruled with four concentric circles of diameters, 12.5,

9.0, 5.5, and 3.5 cm., respectively, and with three diameters, drawn 60 degrees apart. (See figure.) An enlarged duplicate of this ruling was pasted upon a sheet of glass, 23 by 33 cm., which formed the top of the tracing box. · The tracing box was an ordinary wooden box, containing an electric light and so arranged that when a blank piece of paper was placed upon its glass cover the diagram upon its top could be seen through the paper. Since the diagram reproduced that beneath the tank, it was possible to trace quite accurately on a paper upon the box the movements of the planarian in the tank. The top of the box was about 15 cm. above the bottom of the tank, and the light coming through the paper and glass was small, so that the illumination in the box had practically no effect upon the illumination in the tank. When the tracing box alone was lighted, the observer was but just able to make out the contour of the tank.

METHOD

The procedure, in general, was as follows. A rested, but hungry, individual was removed from the dark and placed in about 1 cm. of water in the tank. Then, with only the normal illumination furnished by the light above the apparatus, its course for five minutes was traced as accurately as possible on the tracing box. The subject was then left in the dark for two minutes, after which one of the lower lights in the circle, opposite one side and slightly in front of the animal, was thrown in at the keyboard. As the subject was brought into activity by the light and turned away from it, another light was thrown on in place of the first one, so that the same side of the animal as before was lighted. Thus the planarian was kept constantly turning and turning, while the source of illumination, controlled from the keyboard, kept following it about. As the head is more sensitive to light than the rest of the body, it was found advisable to anticipate the turn, in order to keep the planarian away from the sides of the tank, by throwing on each light about 20 degrees before the long axis of the animal became perpendicular to the radius passing through the light. The light was then left on until the animal had passed 40 degrees beyond the radius. This procedure was possible only in slow, consistent movements; for when the subject turned rapidly it was possible only to follow it hurriedly with the light, often skipping a single

lamp; and again, when the animal became "unruly," it was sometimes necessary to throw on two lights at once in order to keep it from the sides of the tank. However, this latter expedient was seldom resorted to and never continued for more than a few seconds at the longest. After the individual had been subjected to intense illumination from one side for about 30 minutes, it was left in the dark for 2 minutes, and then allowed to glide freely for 5 minutes with non-directive illumination from the light above,—an intensity of illumination approximately one-fiftieth that from one of the lower lights.

An attempt was made in many cases to supplement the observations described by a continuation of the series, alternating thirty-minute periods of right or left illumination with five-minute periods of non-directive illumination; but great difficulty was experienced in finding subjects which would remain active for these extended periods under violent stimulation. Many of the forty-four-minute series described were abandoned because the animals would not remain active. With two of the eight subjects reported upon here (B and E), however, longer series were obtained,— B remaining active, with only occasional mechanical stimulation, for five hours and twenty-two minutes. In this connection, it should be added that, although all the individuals were obtained from the same place, A, B, and E were from a lot taken at a different time from the others.

It was not found possible in all the experiments to keep the exact lengths of periods constant. Now and then, especially in the prolonged series upon individuals B and E, the animal would become sluggish and it would be necessary to terminate the trial before the thirty minutes had elapsed. The four minutes in the dark and the five minutes in the subdued light would, however, frequently refresh it enough to permit the starting of a new trial. In the two prolonged series, whenever the subjects became very sluggish, it was necessary to stimulate them to activity by a slight prod with a stiff hair. In such a case, a subject was prodded only after it had remained inactive for two minutes. This procedure was considered allowable, as the important factors—namely, the direction of turning and the continued exposure of one side to light—were not presumably affected thereby. Very rarely the subject would come to the side of the tank, in spite of the tendency of the light to turn it, and

start to glide along the tank-wall. In these cases it was imme-
diately removed by a section-lifter to the center of the tank.

GENERAL BEHAVIOR

The behavior of the animal under strong illumination from
one side may be described as a continuous, steady glide, occa-
sionally interrupted by "wigwag" movements; but in general,
either by gradual or abrupt turns, it keeps its negative orien-
tation to the light. At times, however, the animal suddenly
moves toward the light, often rapidly making two or three com-
plete turns in this direction before settling back to its previous
course. The behavior of the flat-worm under normal illumina-
tion, following strong, directive illumination, is similar to that
under intense light, except that the general direction of curva-
ture is reversed and that quick, abrupt turning in the direction
opposite to the principal one is less frequent.

DATA

In measuring the records of the paths traced by the plan-
arians the following method was adopted. As the courses were
exceedingly tortuous, they were considered as including no
straight lines; that is to say, as always inclined either to the
right or to the left. All points of inflexion were marked upon
the course. In marking these points no separate account was
taken of very small twists, indicating a change of direction of
less than 45°, unless the length of path was over 2 cm. Any
error involved in this omission is hardly greater than that in-
volved in tracing free-hand the course of a subject often in
rapid motion. Measurements were made of the length of path
and also of the total number of degrees turned through between
successive points of inflexion.

*The symbol "D" is used in this paper to designate throughout
any one series that side of the planarian which is away from the
light during directive illumination; the symbol "L" is used to
designate the side toward the light during directive illumination.*

Table I gives the results of single trials upon eight individ-
uals. The horizontal lines of figures for each individual are
(1) the initial performance under normal, diffuse, vertical illum-
ination, (2) the performance under intense illumination from
the right or left side (as indicated in the column for position of

light), and (3) the final performance under normal illumination. The figures in the four columns under "Course Traversed" give the distance in centimeters passed through while turning to the D-side or to the L-side[6] and the total number of degrees turned through in each direction. The average rate of movement is obtained by dividing the total distance by the total time. The double column at the right of the table gives percentages of excess of distance toward the D- or the L-side. The figures represent the excess of distance passed through while turning toward one side over that passed through while turning toward the other side. The percentage values were found by subtracting the smaller distance from the greater and dividing by the total distance. At the bottom of the table are given the average values for the eight individuals together with the mean variations.

Table II gives the same items for the longer series on individuals B and E, where short periods of normal illumination from above were alternated with long periods of directive illumination. It should be observed that the directive illumination after the first period with E is reversed, thus reversing the significance of the terms D and L as referred to left and right. In the last trials with these two animals it was necessary to prod them after they had remained at rest for 2 minutes. In computing the rates of movement, the time of resting before prodding was included, so that the rates in these cases represent more precisely the activity of the animal than the actual movement.

In Table III the periods under directive illumination of the eight individuals are fractionated. The courses were divided into lengths bearing the same proportion to the total length as ten minutes bore to the total time; *i.e.*, into such lengths as would have been traversed in ten minutes had the planarian moved at a constant rate throughout the period. The excess of movement toward either the D- or the L-side is given in percentages of both linear and angular movement; *i.e.*, there are given both the excess of distance passed through while turning toward one side and the total angular distance turned through.

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[6] It should be observed that this is not the same thing as turning from or toward the light, as the animal may be said to turn toward the D-side or the L-side under non-directive illumination. The terms D and L are fixed for any one series as equivalent to left and right, according as the directive light, when applied, is always applied from the left or from the right.

Table IV shows the excess percentages of both linear and angular distances for the entire series on individual B. The periods of non-directive illumination are given as before (Table II); the periods of directive illumination are fractionated.

ADAPTATION TO LIGHT

In this connection it is desired to show that the planarian, after a continued period of turning under directive light, exhibits a marked tendency to turn in the opposite direction under non-directive light.

As a measure of turning there have been taken the excess percentages of distance passed through while turning, as given in Table I.

It might appear at first thought that the proper measure of the predominance of movement toward one side or the other would be the number of degrees turned through. It must be remembered, however, that the planarian under a strong directive light sometimes exhibits a tendency to turn abruptly toward the light. A similar, although less marked, reversal of direction occurs frequently in the period immediately following that under directive illumination. In this manner the planarian may turn rapidly around two or three times, thus passing in a few seconds through as large an angle toward the light as it has turned through away from the light in several minutes of steady gliding. Since it is most probable that these abrupt turns are not the result of the ordinary directive influences under which the planarian turns, but a specialized response to a continued intensive stimulation, it seems fairer to measure the continuous tendency of the animal to rotate, not by the number of degrees of rotation, but by the distance passed through while turning. The reliability of this substitution of linear for angular measure is attested in a few courses where the abrupt turns were almost entirely absent and the percentages obtained in both ways were very nearly equal.[7]

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[7] For example, with individual F the average curvature toward the light was only 1.07 that away from the light; the excess per cent. based on linear measure was 66%; on angular measure, 65%.

All percentages were computed upon both bases, and both, in general, gave the same result, although those from linear measure were the more striking. The average values for initial non-directive, directive, and final non-directive performance are, respectively, as follows: For linear measure, 5% L, 59% D, and 67% L; for angular measure, 11% L, 32% D, and 69% L.

TABLE I

Ind.	Position of light	Course Traversed				Time	Rate	Excess of Distance	
		Distance		Angle				%	
		cm.		deg.		min.	cm. per min.		
		D	L	D	L			D	L
A	Above	6.9	25.5	320.	830.	3.2	10.1		57.
	Right	*305.7*	*9.9*	*7655.*	*740.*	*30.*	*10.5*	*94.*	
	Above	3.9	11.6	120.	430.	0.9	17.2		50.
B	Above	12.4	19.0	815.	1455.	5.	6.3		21.
	Right	*116.0*	*45.9*	*3605.*	*3460.*	*26.5*	*6.1*	*44.*	
	Above	...	38.7	...	2725.	5.	7.5		100.
C	Above	34.2	29.1	1285.	1060.	5.	12.7	8.	
	Right	*273.2*	*48.7*	*9720.*	*1005.*	*30.*	*10.7*	*70.*	
	Above	...	58.2	...	1850.	5.	11.6		100.
D	Above	13.1	10.3	485.	450.	5.	4.7	12.	
	Right	*115.0*	*25.6*	*2120.*	*1285.*	*30.*	*4.7*	*64.*	
	Above	6.5	10.9	475.	605.	5.	3.3		21.
E	Above	37.7	29.7	895.	920.	5.	13.5	12.	
	Left	*107.7*	*45.6*	*1845.*	*1580.*	*15.*	*10.2*	*41.*	
	Above	5.5	58.7	125.	1555.	5.	12.8		83.
F	Above	16.5	22.8	520.	600.	5.	7.9		16.
	Left	*156.7*	*31.7*	*4320.*	*930.*	*30.*	*6.3*	*66.*	
	Above	3.1	30.5	125.	1095.	5.	6.7		82.
G	Above	30.6	21.3	940.	780.	5.	10.4	20.	
	Left	*213.0*	*73.8*	*5580.*	*4100.*	*30.*	*9.6*	*49.*	
	Above	2.1	45.1	240.	1135.	5.	9.5		91.
H	Above	27.6	25.4	485.	590.	5.	10.6	4.	
	Left	*193.2*	*71.2*	*5320.*	*3435.*	*30.*	*8.8*	*46.*	
	Above	10.1	48.7	325.	1095.	5.	11.8		66.
Mean	Above	22.7 ±10.1	22.9 ±4.5	593. ±266.	824. ±231.	4.8 ±0.4	9.5 ±2.4		5. ±20.
	L	*185.6 ±61.3*	*44.0 ±16.1*	*5021. ±2048.*	*2067. ±1199.*	*27.7 ±3.5*	*8.4 ±2.0*	*59. ±14.*	
	Above	3.9 ±2.6	38.2 ±16.4	176. ±128.	1311. ±550.	4.5 ±0.9	10.0 ±3.3		67. ±12.

It will be observed that five planarians showed at the start some tendency to "rightness" and three to "leftness." On the average, however, they are predisposed only 5% in the L-direction. Under directive light their turning varies from 41%

(E) to 94% (A) away from the light; *i.e.*, they have, on the average, been changed by the change of conditions from 5% in the L-direction to 59% in the D-direction. Under normal illumination, after exposure to directive light, the turning varies from 21% (D) to 100% (B and C), on the average, 67%, in the opposite direction from that preponderant under directive light.

From these results, it seems safe to conclude that the planarian turns from the light because of a difference of intensity of excitation by the light stimulus impressed upon its two sides. As the animal is exposed continuously to the light, the light-recipient organs on the side toward the light source become more nearly exhausted than those on the other side, *i.e.*, the planarian becomes on this side light-adapted. If now the subject is placed under normal, non-directive illumination, the uniformly intense light will excite the light-adapted side less than the other side, thus producing within the organism the conditions that prevail when the opposite side is more intensely stimulated. Hence the animal turns toward the light-adapted side.

That the turning reactions after and during directive illumination are of the same order is also indicated by the fact that the curvature toward the more excited side is in both cases greater, suggesting that the animal reacts in a positive manner toward the side excited by a relatively (although not absolutely) strong and continued stimulus, just as it responds by reacting toward other intensive, continued stimuli. The difference of curvature,—the ratio equals 1.22,—is, however, perhaps not great enough to be conclusive on this point.

Table II presents the complete series of individuals B and E. These results are interesting as a supplement to the material of Table I, although they also raise a question that can be answered only by further experimentation.

With B, it will be observed that strong illumination on the right side was alternated with normal trials for more than five hours. It will be noticed that the "leftness" under right stimulation and the "rightness" under normal stimulation with right-adaptation increases, in general, throughout the first half of the series and decreases throughout the second half, although the change is not perfectly regular. This fact may mean that at first, while the right-adaptation is in process, the reaction be-

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TABLE II

Ind.	Position of Light	Course Traversed				Time	Rate	Excess of Distance	
		Distance cm.		Angle deg.		min.	cm. per min.	%	
		D	L	D	L			D	L
B	Above	12.4	19.0	815.	1455.	5.	6.3		21.
	Right	116.0	45.9	3605.	3460.	26.5	6.1	44.	
	Above	...	37.8	...	2725.	5.	7.5		100.
	Right	90.9	19.5	1540.	1555.	21.	5.3	65.	
	Above	1.0	33.2	140.	1190.	5.	6.3		94.
	Right	85.9	5.6	1770.	540.	18.	5.1	88.	
	Above	0.6	30.5	95.	1560.	5.	6.2		96.
	Right	137.1	1.8	2615.	255.	27.	5.1	98.	
	Above	2.0	28.1	70.	560.	5.	6.0		87.
	Right	78.8	23.6	2555.	2040.	23.	4.5	54.	
	Above	...	32.8	...	830.	5.	6.5		100.
	Right	52.1	29.6	1680.	2515.	21.	3.9	28.	
	Above	...	28.8	...	940.	7.	4.1		100.
	Right	36.7	30.8	1565.	1585.	19.	3.5	9.	
	Above	2.0	19.4	210.	1020.	7.	3.1	.	81.
	Right	49.5	5.4	1305.	505.	18.	3.1	80.	
	Above	13.7	13.6	435.	1235.	5.	4.5	0	0
	Right	20.2	13.9	1065.	965.	16.	2.1	19.	
	Above	2.2	11.3	170.	1535.	12.5	1.1		67.
	Right	64.5	9.1	2070.	510.	25.	2.9	75.	
	Above	6.0	5.3	670.	565.	5.5	2.1	6.	
E	Above	37.7	29.7	895.	920.	5.	13.5	12.	
	Left	107.7	45.6	1845.	1580.	15.	10.2	41.	
	Above	5.5	58.7	125.	1555.	5.	12.8		83.
	Right	171.0	9.2	4740.	330.	17.	10.6	88.	
	Above	47.0	5.4	1345.	165.	5.	10.5	80.	
	Right	115.0	5.8	3255.	425.	20.	6.0	91.	
	Above	31.0	...	1005.	...	5.	6.2	100.	
	Right	84.8	13.8	4550.	385.	15.	6.6	72.	
	Above	31.8	...	1000.	...	5.	6.4	100.	

comes proportionately more pronounced; but that later, with the right-adaptation complete, the left side, which during horizontal illumination by no means remains in complete darkness, but is on the contrary quite strongly illuminated, also becomes partially light-adapted, thus decreasing the difference in excitation between the two sides, and hence the pronounced character of the turning.

After planarian E had become adapted to light on the left side, it was exposed to light in three successive trials on the right side. The animal turned from the light consistently, but, instead of reversing direction under normal illumination, it continued to turn decidedly toward the left. It seems as if, at the end of the second trial, the adaptation on the right side could certainly not be less than that on the left, and the animal might be expected to turn to the right or at least to show no preference for one side over the other. Why the leftness persisted is a question that can be decided only by experiments upon a number of individuals.

The distance percentages in Table III show that during the first total period of lateral stimulation the animal tends to move less and less away from the light, the excess movement from the light being, on the average, 78%, 56%, and 38%, respectively, in the three successive fractions. This change is probably due in the main to increasing light-adaptation, although it may be influenced by compensatory movements and decreased sensitivity under fatigue. It seems safe, however, to say that the effect of light-adaptation reaches a maximum within the first ten minutes' exposure. In planarian E, the effect was very marked at the close of a fifteen-minute period.

It cannot be said that complete adaptation on both sides was reached at any time, although the absence of the usual response under non-directive illumination in the eighth and tenth trials of B (0% and 6% D) suggests that this condition may have been approximated in the preceding four hours of experimentation.

The adaptation appears to be true adaptation in that it is not permanent. After twenty-four hours, C, F, G, and H showed practically no preference for one side over another. A, B, D, and E were too fatigued to respond. After forty-eight hours A and E appeared normal and showed practically no preference

TABLE III

Ind.	Position of Light	Frac-tion	Excess of Movement				Estimated Time
			% Distance		% Angle		min.
			D	L	D	L	
A	Right	1	90.		85.		10.
		2	100.		100.		10.
		3	92.		72.		10.
B	Right	1	61.		39.		10.
		2	22.			25.	10.
		3	48.			10.	6.5
C	Right	1	97.		96.		10.
		2	72.		88.		10.
		3	29.			17.	10.
D	Right	1	63.		43.		10.
		2	77.		30.		10.
		3	50.			48.	10.
E	Left	1	65.		31.		10.
		2		9.		30.	5.
F	Left	1	78.		72.		10.
		2	67.		65.		10.
		3	54.		53.		10.
G	Left	1	90.		84.		10.
		2	59.		56.		10.
		3		3.		19.	10.
H	Left	1	78.		63.		10.
		2	62.			1.	10.
		3		1.		18.	10.
Mean	L	1	78. ±11.		64. ±20.		
		2	56. ±25.		23. ±44.		
		3	38. ±26.		2. ±35.		

for either side. D was injured and had to be discarded. B was still fatigued. After approximately four days B showed a slight preference for the left.

REVERSAL OF REACTION

It has already been noted that the planarian under directive light frequently turns abruptly toward the source of illumination in a manner, which, by reason of its quickness and suddenness, is quite different from the slower continuous turning from the light. Although less markedly, the animal also tends to

reverse direction abruptly during its course under normal illum-
ination after directive light. This does not appear in the course
under normal illumination before exposure to directive light.
Since the preponderance of abrupt turns in one direction in-
creases the average curvature of the path in that direction, the
difference can be stated numerically as follows: For the eight
subjects under initial, non-directive light the curvature in the
L-direction was 1.08 times that in the D-direction,—*i.e.*, very
nearly equal. Under directive illumination the L-curvature was
1.95 times the D-curvature. Afterward, under final, normal
light the D-curvature was 1.22 times the L-curvature. Thus,
we see that the curvature is greatest in the direction of least
turning.

This curious type of behavior appears similar to that de-
scribed by Pearl[8] as the response of the animal to repeated
strong mechanical stimulation. After repeatedly giving the
negative reaction in response to strong mechanical stimulation
of the anterior end, it "finally jerks back with a strong longi-
tudinal contraction, and turns the anterior end through a con-
siderable arc, so that it points in . . . an entirely opposite
direction to that of the previous reactions." "This reaction,"
Pearl continues, "appears as if, after the animal had tried in
vain to get away from an uncomfortable stimulus by its ordinary
reaction, it finally tries a wild jump in the opposite direction.
This curious change in the reaction induced by a repetition of
strong stimuli . . . indicates the effect of the organism
as a whole upon its reflexes."

It is not, however, by any means necessary to assume that
the animal, failing to get relief by the usual negative response,
alters its mode of behavior, implying, as this does, consciousness
other than the simplest. It is quite conceivable that the abrupt
reversals of direction for brief periods, the "wild jumps," are
forms of a compensatory movement, which acts as a relief, not
for the continued stimulation, but for the continued movement
away from the stimulus. Who has not, after prolonged, unac-
customed bending of the body forward in the removal of potatoes
from the ground or tacks from the carpet, stood erect and bent
the body far backward in order to "take the kink out of his
back," before resuming his labors. The planarian directs its

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[8] *Quar. Jour. Micr. Sci.*, *46*, 1903, p. 580.

course by means of longitudinal muscles, which warp the worm along its long axis, and thus steer it to one side. It is quite possible that these muscles, after the continued contraction involved in prolonged movement to one side, become cramped, and that there follows what is probably a natural physiological co-ordination, when the muscles on the other side contract suddenly and strongly, stretching the fatigued muscles. This explanation involves the assumption of a simple physiological co-ordination, but it avoids the implication of a complex consciousness. Nor is it really incompatible with Pearl's suggestion that it shows "the effect of the organism as a whole upon its reflexes."

Let us carry further the analogy to muscular cramp. As the amateur agriculturist works farther and farther along the row of potatoes, he pauses oftener and oftener to stretch until a certain point is reached; thereafter, provided the stimulus is strong enough to compel a continuation of the work, he pauses less and less often and presently not at all. The muscles "get set;" he now feels as if he could not straighten out. A similar phenomenon, although not strictly analogous, can be seen in continued walking, where the rests for the unaccustomed walker become more and more numerous, until at last, if he continues, the walker "strikes his stride" and does not rest again.[9] Proceeding upon this analogy, we should expect the compensatory movements of the planarian to increase up to a certain point, then decrease, finally dropping out altogether, provided, of course, that the animal remains active for a sufficiently long time.

The increase in compensatory movement appears in Table III. Here we must consider the percentages based upon angular movement, as those based upon linear movement largely exclude the effect of abrupt turns and were for that reason used in consideration of light-adaptation. There is shown, on the average, a reduction of turning in the D-direction from 64% to 2%. This reduction may be considered as due in part to light-adaptation and in part to an increase in compensation. We have already considered that the effect of light-adaptation upon the

[9] The writer has a detailed record of a fifty-mile walk, taken by two persons, without any systematic practice in the preceding six months. The stops for rest, although not numerous, became more and more frequent throughout the first part of the route, until the last twenty-two miles, during which no stops at all were made. In this last stage the pauses for water or for inquiries were accompanied by a continuation of the walking movements with the legs.

D-turning was to reduce it from 78% to 38%. Very roughly, then, the effect of compensatory movement may be considered to be proportional to the difference between these two sets of figures; i.e., 14% at first, 36% at the end.

The increase in compensation is greater for many individuals than the average would lead one to expect. Six individuals (B, C, D, E, G, and H) in the last fraction actually turned through a greater angle toward the light than away from it. This change of direction is entirely as might be expected, so long as the preponderance of preceding continuous movement (as measured by the percentages of distance) has been away from the light, for it is obviously intrinsic in compensatory movement that it should be in the opposite direction from the greater amount of movement.

An apparent exception in the case of E may be explained as follows. In the first ten minutes, 65% of D-movement may have resulted in sufficient compensation to reduce the angular excess in the same fraction to 31% in the D-direction and to change the angular excess in the succeeding five minutes to 30% in the L-direction. By this time, however, the light sensitivity may have become so reduced as to reduce the continuous movement almost to zero. The actual distance toward the light passed through in the compensatory turns would account for the positive value of 9% in the L-direction. The explanation in the other cases is obvious.

That compensation finally disappears is shown, it is thought, in Table IV. In the column of angular measure it will be observed that the planarian at first changes in each period from the D- to the L-direction under directive light from the right, but that later the tendency is to turn first in the L- and then in the D-direction. This behavior accords perfectly with our hypothesis of the final lapse of compensation, if we assume that in each of the later periods the planarian is just so fatigued for D-turns that it responds at the start with a high degree of compensation, which, under increased fatigue, soon drops out altogether. That it repeats this course in successive periods may be due to the fact that the interval of turning under normal light in the opposite direction partially rests it.

It thus appears that we can account for all the facts observed by a theory of abrupt turns given in compensation to preceding

TABLE IV

Ind.	Position of Light	Period and Fraction	Excess of Movement				Estimated Time
			% Distance		% Angle		min.
			D	L	D	L	
B	Above	1		21.		28.	5.
	Right	1–1	61.		39.		10.
		1–2	22.			25.	10.
		1–3	48.			10.	6.5
	Above	2		100.		100.	5.
	Right	2–1	87.		59.		10.
		2–2	46.			16.	11.
	Above	3		94.		77.	5.
	Right	3–1	97.		64.		10.
		3–2	81.		38.		8.
	Above	4		96.		89.	5.
	Right	4–1	93.		69.		10.
		4–2	100.		100.		10.
		4–3	100.		100.		7.
	Above	5		87.		78.	5.
	Right	5–1	27.			17.	10.
		5–2	74.		35.		13.
	Above	6		100.		100.	5.
	Right	6–1	27.			40.	10.
		6–2	28.		7.		11.
	Above	7		100.		100.	7.
	Right	7–1		31.		8.	10.
		7–2	52.		11.		9.
	Above	8		81.		66.	7.
	Right	8–1	68.		13.		10.
		8–2	96.		68.		8.
	Above	9	0	0		54.	5.
	Right	9–1		30.		23.	10.
		9–2	100.		100.		6.
	Above	10		67.		80.	12.5
	Right	10–1	39.			24.	10.
		10–2	100.		100.		10.
		10–3	100.		100.		5.
	Above	11	6.		8.		5.5

continuous movement in the opposite direction. Pearl seemed to think that the positive response to continued strong stimulation was the result of the stimulation itself rather than of the movement caused by the stimulation. If Pearl's interpretation were correct, it should be possible after long exposure to directive light to cause the planarian to turn always toward the stimulus. Upon a theory of compensation the rotation could be brought only to neutrality; the sign of the reaction could not be reversed. In the subjects studied the sign of the reaction was certainly not reversed; yet there is no positive evidence that it could not have been. The theory of compensation is offered merely because it is simpler and more comprehensible and, at the same time, it is adequate to all the facts so far observed.

FATIGUE

The effect of general fatigue upon the rate of movement can be observed in the series with both B and E (Table II). Here the rate under either normal or intense directive stimulation decreases almost uniformly; but the rate under intense illumination is almost invariably less than that under normal illumination at the same part of the series. This latter fact appears with all the individuals studied, the average normal rate before and after directive illumination being 9.5 and 10.0 cm. per min., respectively; and during directive illumination, 8.4 cm. per min. This difference agrees with that observed by Parker and Burnett,[10] who found that a rate of 6.7 cm. per min. under vertical illumination was reduced to 6.24, when the planarian was started directly toward the light and continued turning away throughout its course.

CONSCIOUSNESS

Of interest to the comparative psychologist is this question: If we impute consciousness to the planarian in connection with the negative reaction, what is this consciousness like? It is apparent that the response of the animal is not to the absolute intensity of a stimulus, but to some resultant of the relative intensity of two stimuli; for, under the general distribution of light with the intense illumination, the animal moves toward

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[10] *Loc. cit.*, p. 384. *Cf.* also Walter, H. E., *loc. cit.*, pp. 56ff., 75ff.

a side which, it would seem, is more strongly excited than that from which it moves away under weak, diffuse illumination. It is not necessary to assume a two-process consciousness involving an opposition of the conscious representatives of the excitations upon both sides. The opposition may be entirely non-conscious, so that the reaction of the animal may be regarded as merely the physical resultant of two unequal, opposing forces, a resultant which might be represented in consciousness by a single process, just as the resultant of red and green stimulation of the retina is accompanied by a single sensation of the quality aroused by the predominant component.

If we push this analogy further, we are led to assume a qualitative difference between the process accompanying the response toward the left and that accompanying the response toward the right,—just as there exists a qualitative difference between red and green. Such a consciousness of "leftness" and "rightness," involving, as it does, an elementary two-quality form of spatial consciousness, it is, nevertheless, not necessary to assume. To be sure, the substitution by the planarian under continued strong stimulation of a reaction toward one side for that toward the other appears to constitute a modification of behavior that comes at least as near implying consciousness as does any other form of behavior in the planarian;[11] and, if we assume that the change in response is the direct result of continued stimulation, we may expect it to be paralleled by a change in conscious content, say, from a simple "get-away-to-the-right" process to a simple "get-away-to-the-left" process. If, however, we accept the notion that the change of response is due merely to muscular compensation, it is no longer necessary to postulate two avoiding reactions aroused by the same stimulus nor the resulting spatial differentiation. If there is a conscious concomitant to the negative reaction, it may be no more than a single "get-away" process.

We may deny the spatial character of the change of content accompanying the reversal of reaction, and yet not deny the change itself. On our simplest hypothesis, we assume a muscular contraction as the result of great fatigue in other muscles,— a co-ordination as complex as that involved in the ordinary

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[11] In unpublished work by Professor Bentley and the writer the "very characteristic" gripping reaction, forming "an integral part of the normal food reaction," described by Pearl, *loc. cit.*, pp. 624ff., has not been observed.

turning away from a stimulus and presumably of equal benefit to the organism. If we postulate a " get-away " process for the first reaction, we may assume a " stretch " process, different in quality, for the second. Consciousness would then consist of the mere alternation between two qualitatively different processes, paralleling the alternation between the two kinds of reaction, or possibly merely the flashing in of the processes at the moment of change.[12]

SUMMARY

Planarians, if subjected to continued, intensive, directive light, continue turning from the source of light. If they are immediately placed in non-directive light after being in directive light, they turn consistently in the direction from which the light at first came. This behavior indicates that the planarian becomes light-adapted on one side during the exposure to directive light, and later, under a uniformly applied stimulus, turns toward the light-adapted side, because that side, on account of its decreased sensitivity, is excited to a less degree than the other, just as would be the case were the animal subjected to directive light from the other side.

After continued turning in one direction under directive light, the planarian tends to make frequent abrupt changes of direction toward the light. These abrupt turns increase in frequency for a while, but, if the stimulation is very long continued, may finally disappear altogether. They may be explained as a form of compensatory muscular movement, initiated

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[12] An attempt was made to duplicate planarian conditions upon two human observers, who, with only diffuse light admitted to the eyes through a tracing-cloth blind, the left eye in addition very darkly screened, an electric light fastened to the body in front of the right shoulder, and the arms and legs bound so as to admit only of very limited movement, were instructed " to leave the mind as blank as possible, to move in response to any strong impulse that might be felt, and, when not strongly impelled to do otherwise, to turn from the light." The result was a slow shuffling forward to the left with a tendency, when interrupted by an object, to move backward (compensatory movement?) for a little before going forward again. The introspections showed a scant consciousness, with the left-forward movement carried throughout in unclear kinesthetic terms. At the pauses, there was a heightened consciousness, with an alternation between the left-forward and backward impulses, both carried kinesthetically, in which the latter ofter supplanted the former, with accompanying backward movement. Although the kind of muscular movement involved is not exactly analogous to that in the planarian, it is believed that the similarity of the introspective account to that derived for the planarian argues in favor of the latter. *Cf.* a preliminary report on *The Use of the Maze in Comparative Psychology*, by L. M. Day and the writer, *Psych. Bull.*, *9*, 1912, p. 60.

as a relief from the continued contraction of the muscles already involved in turning.

The rate of movement decreases with the increase of general fatigue, and is less under intense, opposing, directive illumination than under weak, non-directive illumination.

The conscious experience, concomitant with the turning from the light and the sudden reversals toward the light,—if there is consciousness involved at all,—is not necessarily of a more complex form than that of an alternation between two qualitatively different processes, or a flashing in and out of these processes at the moment of the change of reaction.

THE MAMMALIAN EYE

S. B. VINCENT

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For the past ten years comparative psychology has busied itself with animal experimentation and in such experimentation, directly or indirectly, vision has played a leading rôle. Whether the problem has been one of discrimination, imitation, or the acquisition of some co-ordination like the maze, sight has been always a factor, if not the important factor with which to reckon. In spite of this, knowledge, structural or functional, of the sense involved has been far from adequate if we may judge from the way the work has been conducted and from the results which have been expected.

It has been generally agreed that the vision of the white rat is poor, yet in looking for anatomical, physiological or psychological data to support such contention or to show in what respects it was poor, where it failed, no entirely satisfactory answer was found anywhere.

On the side of psychology, Mr. Small, speaking of some feats of climbing before the eyes of the rats were open says, "Now as the same movements are used in orientation after the eyes are open as before one is led to conclude that the influence of the eye in the orienting process is very slight." [1]

Mr. Watson thinks vision plays little part in the maze association. He says, "Many times we have taken our normal rats and have flashed strong lights in their eyes. We never got the slightest quiver of an eyelash by so doing much less reaction of the animal as a whole." [2]

Mr. Yerkes concludes that sight is of little importance in the life of the dancer, "that movements and changes in bright-

[1] Small, W. S. Development of the White Rat. *Amer. Jour. of Psych.*, 1899, Vol. 11, p. 63.

[2] Watson, J. B. Kinaesthetic and organic sensations: their rôle in the reactions of the white rat to the maze. *Psychological Review, Mon. Sup.*, 1907, Vol. 8, No. 2, p. 90.

ness are the only visual conditions which to any considerable extent control the activity of the animal." [3]

Mr. Waugh [4] has studied vision in the white mouse. Neglecting for the time his experiments and conclusions on color vision let us consider those on form and distance. The forms to be discriminated were a circle and a cross, cut in black cardboard and illuminated by lights from behind. He only finds discrimination present in one instance, and in this case the per cent. of right choices in 130 trials was only 69 +. He does not give us the exact order of alternating the forms. May not this rat have partly learned the order?

He tested distance discrimination by having animals jump from a wooden disk set at different heights above a table whose surface was varied in color. The time elapsing between the placing of the animal and the jump was taken as an evidence of the animal's ability to discriminate distance. In the first experiment the time increased with the distance, but in the second and third, where there was a glass surface over the table below, the time was unusually long even when the distance was not increased above 10 cm.

Mr. Waugh anticipates the objections to taking the time of the reaction as proof of the discrimination of distance, but he says nothing about olfaction which is also a distance sense and probably a very keen one in these animals. The very fact that glass, which is as non-odorous as anything we know, should present such difficulties would suggest an odor criterion in this case.

He speaks of the short range of vision in the mouse, but gives no anatomical data to support this belief and his experiments with depth give none.

His results were practically negative so far as the discrimination of either form, distance or depth were concerned, but he neglected, as others who have experimented with animals have neglected, to establish first a normal focal distance or distance of accommodation. The distances at which Mr. Waugh tried his animals for discrimination of depth were 2, 4, and 6 in.

[3] Yerkes, R. M. The Dancing Mouse. New York, 1907, p. 198.
[4] Waugh, K. T. The Rôle of Vision in the Mental Life of the Mouse. *Jour. of Comp. Neur. and Psych.*, 1910, Vol. 20, p. 570.

Hypermetropic animals, and probably all animals are hypermetropic in the wild state, may well fail to discriminate form at short range. The same criticism would apply in a lesser way to discriminations of brightness and color, especially where the differences are slight.

Mr. Watson's rats [5] and Miss Allen's guinea pigs [6] failed to discriminate food at sight and experiments with the dancing mouse by Mr. Yerkes [7] for discrimination of form gave negative results, but Messers. Thorndike [8] and Kinnaman [9] obtained discrimination of form from monkeys and Porter [10] and Rouse [11] from sparrows, cow-birds and pigeons. The monkey's eye anatomically is very similar to that of man and birds possess a well defined fovea, sensitive area and a retina with both rods and cones. A fovea is most likely essential to form discrimination. although in discussing the lack of such power, as has been said, we may have to face the charge of providing forms for discrimination which are entirely strange to the animal's life and habitual discriminations if it makes any.

These studies seemed to confirm the general belief that the vision of these animals was not of the strongest, still we were not shown where the weakness lay. The following tabulation is the result of a search for such anatomical, physiological material and gives in this form, so far as found, the answer sought. The facts are compiled chiefly from the work of Chievitz,[12] Lindsay Johnson,[13] Slonaker,[14] and Harris.[15]

Dr. Johnson not only examined the eyes of the animals with

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[5] Watson, J. B. Animal Education 1903, p. 58.

[6] Allen, Jessie. Association in the Guinea Pig. *Jour. of Comp. Neur. and Psych.*, 1904, Vol. 14.

[7] Yerkes, R. M. *Op. cit.*, p. 180.

[8] Thorndike, E. L. Imitation in Monkeys. *Amer. Jour. of Psych.*, 1902, Vol. 13, p. 98. Animal Intelligence, New York, 1911.

[9] Kinnaman, A. J. Mental Life of two Macacus Monkeys in Captivity. *Amer. Jour. Psych.*, 1902, Vol. 13, p. 98.

[10] Porter, J. P. The English Sparrow and Other Birds. *Amer. Jour. Psych.*, 1906, Vol. 17, p. 264.

[11] Rouse, J. E. The Mental Life of the Domestic Pigeon. *Harvard Psychological Studies*, 1906, Vol. 11, p. 581.

[12] Chievitz, J. H. Ueber das Vorkommen der Area Centralis Retinae. *Arch. f. Anat. u. Physiol.*, Anat. Abtlg., 1891, p. 311.

[13] Johnson, G. L. Contributions to the Comparative Anatomy of the Mammalian Eye. *Phil. Trans. Roy. Soc.*, 1901, Vol. 194 (B), pp. 1–82.

[14] Slonaker, J. P. A Comparative Study of the Area of Acute Vision. *Jour. of Morph.*, 1897, Vol. 13, pp. 445–494.

[15] Harris, W. H. Binocular and Stereoscopic Vision. *Brain*, 1904, Vol. 27, p. 106.

the ophthalmoscope but determined the refraction by retinoscopy and measured the angle of divergence of the optic axes with a specially devised goniometer. Chievitz determined the sensitive area microscopically for many animals, including 20 mammals. Johnson with the ophthalmoscope for 182 mammals and Slonaker for 93 vertebrates including 18 mammals. Harris bases his discussion of binocular and stereoscopic vision upon evidence of complete or incomplete decussation of the optic nerves. He studied the ocular movements and the pupil light reflexes and gathered his evidence from operative experimentation and from examination of normal animals.

The tabulation includes facts from other mammals for purposes of comparison, and those animals have been chosen which have been most used in comparative psychology. A discussion of the data may be useful since there are so many different factors which help to make vision good or bad.

The color of the fundus is the first thing noticed in an ophthalmoscopic inspection. As will be seen it varies greatly in different orders and species. The significance of this color is as yet but imperfectly understood, although it is thought that it may prove to be in some way connected with the color vision of the animal.

Another thing which the ophthalmoscope reveals at once is the shape and size of the optic disc. Large discs and opaque nerve fibres mean blind areas on the portion of the visual field affected and hence must be noted among the facts which contribute to poor vision.

None of the mammals below the primates possess foveas, but there is often a definite sensitive area whose size and position is important for vision. This has been determined by Johnson for a number of forms with the ophthalmoscope and microscopically for many forms by Chievitz, Slonaker and others. It seems to be larger in those animals where the divergence of the axes is great and when combined with nearly spherical lenses and large corneas it gives the animal a wide range of vision which may possibly be binocular. Probably considering the mode of life such wide range is of more importance than the sharp focus made possible by a fovea; but the fovea, when it does appear, is accompanied by only slight divergence of the optic axes—a

condition which most nearly approaches the human for sharp vision.

Acute sight, however, depends also upon the shape of the lens, cornea and pupil. A large cornea permits more oblique rays to enter the eye, while large spherical lenses correct the distortion which might result from the unequal refraction. The size of the pupil is perhaps of not so much importance as its power of dilation. The round pupil is characteristic of the higher types of eyes. It has been found that horizontally oval or round forms react less readily to mydriatics and less quickly to light than vertically oval or round forms. The pupils of ungulates are very unresponsive to either drugs or light.

We need not pause long to consider divergence. Laterally placed eyes, of course, preclude stereoscopic vision and parallel axes are found only in man and monkeys. The divergence is greatest, according to Johnson, in rabbits where the fields of the two eyes probably overlap both in front and behind. It is said that a squirrel can see any one approaching directly behind it.

This ability to see on all sides gives the animal greater security from enemies and is accompanied in the wild state by hypermetropia in all animals below simia, according to Johnson. But both he and others say that refraction becomes variable under domestication.

Johnson also remarks that there is complete absence of convergence below simia and that monkeys converge for only a slight period. He believes that animals below simia do not move their eyes for visual purposes or for purposes of convergence. Harris disputes this and contends that there is a degree of convergence and of binocular vision especially in animals which pursue their prey and have to follow it with their eyes.

Harris studied stereoscopic and binocular vision by means of experimental work to demonstrate the incomplete or complete decussation of the optic nerve fibers and also made microscopic studies of degeneration. He believes that where there is incomplete decussation there is at least the possibility of binocular vision. In these cases the eyes are set rather far forward. He also used the light·reflex to confirm nerve section and says that "Sluggishness of pupil reaction seems generally to be

accompanied by a low standard of acuteness of vision as in ungulates and rodents."

Popular belief as to the significance of the rods and cones seems to ascribe to the one the specific function of vision in a dim light, colorless vision, and to the other in some hypothetical way color vision. The facts of peripheral vision, color blindness and night vision are brought to the support of this theory. More recent work seems to be greatly modifying the old conceptions of retinal structure and making the distinctions between rods and cones less absolute. The reader is referred to the studies of Hess,[16] Cajal,[17] Bernard,[18] and Cameron.[19]

When the figures giving the refractive indices for lens and eye media are noted it will be seen that there can be little power of accommodation in most of these forms where the refractive indices so nearly approach each other. The figures for man are lens (total refractive index) 1.437, fluid media, 1.336. In fishes the accommodation is brought about by altering the distance between the lens and retina. The rat has no known mechanism for any such purpose nor has any such alteration been observed.

In the light of this discussion what shall we conclude about the rat's eye. As arguing against its good vision we have a thread-like optic nerve, opaque nerve fibres, no sensitive area, no fovea, no eye movements demonstrable,[20] a pupil which reacts very sluggishly to light, a divergence of the optical axes of 60 to 84 degrees, and in the wild state extreme hypermetropia. That there may be an occasional variant from this last under conditions of domestication is true, but the great curvature of the cornea and sphericity of the lens are indications against its being of frequent occurrence.

And what shall we say as to the conduct of experimentation? First, we must establish for all experimentation employing vis-

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[16] Hess, R. Ueber der Bau und Zapfen der Wirbeltiere. *Deutsch zool. Ges.,* 1903, Bd. 13, S. 33–41. See also numerous papers of C. Hess.

[17] Cajal, Ramón y. Histologie du Système Nerveaux de l'Homme et des Vertébres, Fr. ed., 1911.

[18] Bernard, Henry M. Studies in the Retina. *Quarterly Jour. Mikro. Sc. N. S.,* 1903, Vol. 46, pp. 25–75; Vol. 47, p. 303.

[19] Cameron, John. Farther Researches on the Rods and Cones of the Retina. *Jour. Anat. and Physiol.,* 1911, Vol. 46, pp. 45–53.

[20] I have never seen a rat's eye move under normal conditions. A very slight nystagmus may be produced by rotation showing that there is some power of movement.

TABULATED DESCRIPTION OF THE FACTS OF VISION IN THE EYES OF A FEW MAMMALS

	FUNDUS AND TAPETUM-LUCIDUM	SHAPE AND COLOR OF OPTIC DISC	SENSITIVE AREA	FOVEA	SHAPE OF PUPIL	DIVERGENCE OF OPTIC AXES	REFRACTION	STEREOSCOPIC VISION	RODS AND CONES	DECUSSATION OF OPTIC NERVE	PUPIL LIGHT REFLEX	REFRACTIVE INDEX OF LENS[21]	REFRACTIVE INDEX OF FLUID MEDIA
Primates, (Macacus cereopithicus)	Dark chocolate bounded by darker macular area surrounded by bright circular reflex ring.	Round or vertically oval pink disc, semi-opaque nerve fibers.	Small compared with other mammals.	1 mm. toward nasal side of optic nerve.	Circular.	Parallel.	Myopia exceedingly rare, practically no astigmatism.	Simiæ the only mammals which possess the power of convergence. Monkeys only able to converge for a very short period.	Present.		Quick reflex. Consensual reaction.	1.333 8 variation .0031.	1.33322 variation .0032
Carnivora, (Felis domestica)	Several zones, center usually golden yellow, intermediate green, periphery red, brown or purple, stippled with minute dots.	Cup disc, round, varying in color, always surrounded by bright colored fringe, usually emerald green.	Round, toward temporal side of nerve entrance.	Fovea (Krause)	Round, contracting to vertically oval or straight line.	7 to 9 degrees.	No myopia in wild state, great variability under domestication, astigmatism.	Complete absence of power of convergence among wild animals and domestic animals, unless specially trained, do not move their eyes either for convergence or for visual purposes—no habitual convergence below Simiæ.	Present, rods and cones present, cones better in cat, dog.		Quick light reflex. Fair consensual reaction.	1.33906 variation .00107	1.33909 variation .00106
Carnivora, (Canis familiaris)	Same as above, characteristic of night animals; great variation in domestic dogs.	Great variation.	Round area toward temporal side of nerve entrance.	None.	Round.	15 to 25 degrees.	Same as above.	See above.	Present.		Sluggish pupil reflex. Fair consensual reaction.	1.33483 variation .0003.	1.3349 variation .0005.
Carnivora, (P lotor)	Central area covered with yellow patches, darker periphery.	Vertically oval.	Band-like area, horizontally across retina above nerve entrance; 5 to 7 mm.	None.	Circular, concentric arrangement of lens fibers.	25 to 30 degrees.		See above.	Present.			1.3338 variation .00163.	1.33378 variation .00105.
Ungulata, (P equidae)	Central zone of yellow and green, stippled with purple and brown; peripheral zone violet and brown, variable.	Horizontally oval, pink, opaque nerve fibers.		None.	Horizontally oval, iris hardly sensitive to mydriatics but sensitive to strong light.	10 degrees.	Myopia most prevalent, astigmatism.	See above.	Cones long oval, much shorter than rods.	About one-sixth of the fibers do not cross.	Sluggish pupil reflex to light. Contraction much greater on side stimulated.		
Rodentia, (Myorpha)	Fundus uniform in color, no tapetum-lucidum, (albino pure white).	Small, chalky white, in rat reduced to a mere point, opaque nerve fibers, optic nerve hardly the size of a cotton thread.	No area	None.	Round, contracting to a pin's head, lens made up of concentric circles, cornea perfect hemisphere extending to center of globe.	60 to 64 degrees.	Rodents markedly hypermetropic in wild state, great variability in refraction and astigmatism under domestication.	See above.	Rodents without cones.	Practically complete decussation.	Sluggish reaction, limited to side stimulated.		
Rodentia, (S ludoviciana)	Pink with tint of gray due to opaque nerve fibers. No tapetum.	Elongated, white, depressed, both relatively and absolutely larger than any other animal examined.	Small, oval, above and to temporal side of retina.	None.	Lens nearly spherical, pupil invariably round.	60 to 80 degrees.	Markedly hypermetropic, 2 to 5 diopters.	See above.	See myorpha.				
Rodentia, (H cavidae)	Buff or slaty gray devoid of retinal vessels. No tapetum.	Chalky, white round, large. Opaque nerve fibers.		None.	Circular.	55 degrees.	Variable under domestication.	See above.	See myorpha.				
Rodentia, (Leporidae)	Vermillion red.	Round, oval white disc, considerably above visual axis. Opaque nerve fibers.	Band-like area, horizontally across retina, immediately below nerve entrance.	None.	Circular.	60 to 80 degrees.	Hypermetropic in wild state, marked myopia under domestication, no astigmatism.	See above.	See myorpha.			1.33045 variation .00361.	1.33060 variation .0032.

[21] Freytag, Gustav. Die Brechungsindices der Linse und der flussigen Augenmedien bei Katze und Beim Kaninchen. *Archiv. f. verg. Opth.*, 1910, Vol. I.

ual discrimination normal focal distances for all the animals used if our results are to be at all trustworthy; second, if the conditions so nearly approach those of peripheral vision, the stimulus should preferably be a moving one; third, the light conditions should be those to which the animal is best adapted; and fourth, we should not expect sharp discrimination of form from eyes such as those we have described.

BEHAVIOR OF FIRE-FLIES (PHOTINUS PYRALIS)? WITH SPECIAL REFERENCE TO THE PROBLEM OF ORIENTATION

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INTRODUCTION

The production of light in living tissue, although confined to relatively few species, is widely distributed among living organisms. It is rather common in molds and bacteria and it is found in representatives of all classes of animals including vertebrates where it is especially common among certain groups of fishes.

In some cases, the molds for example, it is exceedingly difficult to conceive of any possible biological significance that luminescence may have. In others it is highly probable that it is closely associated with fundamental phenomena in the life of the organisms. All sorts of suggestions have been offered with reference to the function of the production of light in different species. In some it is considered to be mainly a secondary sexual characteristic; in others it is supposed to serve primarily as a lure for prey; and in still others as protection against enemies. Among the most novel of such suggestions that I have seen is one presented by Dubois, a prominent naturalist, who maintains that certain tropical birds capture fire-flies and fasten them to the soft clay walls of their nests and that the light which they produce while thus situated protects the nest against snakes.

While some of the hypotheses which have been offered will probably eventually be found to hold for many different species, only in very few cases has the function of luminescence thus far been well founded, in fact, it has been clearly established only in one case.[1] Galloway found (1908) that in the annelid,

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[1] After the main part of this paper was completed there appeared an article by McDermott, in the *Canadian Entomologist*, Dec., 1911, in which the author presents strong evidence in support of his contention that luminescence in the fire-flies, Photinus pyralis, P. scintillans, and P. consanguineus, functions primarily as a secondary sexual character. In this interesting paper McDermott also calls attention to observations made by Osten-Sacken on Photinus pyralis in Washington, D. C., 1861. These observations, which were described in the *Stettiner Entomologische Zeitung*, also demonstrate fairly conclusively that in this species the production of light functions in mating and this appears to be the first record bearing on the biological function of this phenomenon that is in any way conclusive.

Odontosyllis enopla, just before mating, which probably occurs periodically about every 26 days during several summer months, the females are found at dusk swimming about near the surface of the water. At first they are only very slightly luminous, but later they quite suddenly become acutely phosphorescent, particularly in the posterior three-fourths of the body. At this phase they swim rapidly through the water in small, luminous circles two inches or more in diameter. "The male first appears as a delicate glint of light, possibly as much as 10 or 15 feet from the luminous female. They do not swim at the surface, as do the females, but come obliquely up from the deeper water. They dart directly for the center of the luminous circle and . . . seize the female with remarkable precision, when she is in the acute stage of phosphorescence." No more light is produced by either individual after mating. Galloway leans toward the opinion that the luminosity in the male is useless and that phosphorescence is a by product of a form of metabolism. I assume he would maintain that the origin of this phenomenon was accidental and had no connection with its present function in mating.

In all other instances the conclusions as to the function of luminescence are either purely speculative or are based mainly upon structural evidence such as the more highly developed and larger eyes in the active male fire-flies as compared with the relatively small ones in the comparatively inactive females. Mangold says (1910, p. 328), "Leider sind wir in der Frage nach der ökologischen Bedeutung des Leuchtens fast ausschliesslich auf Hypothesen angewiesen."

It is not my purpose to review the very extensive literature on the subject of luminescence in organisms in its different phases. This has recently been very well done by Mangold (1910) who has brought together in his bibliography 649 titles, an enormous number, testifying to the general interest in the subject.

MATERIAL

I took up the study of the behavior of fire-flies [2] in the neighborhood of Smithsburg, Western Maryland, early in June, 1911.

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[2] Dr. F. H. Chittenden of the Bureau of Entomology, Washington, D. C., kindly identified a number of specimens of fire-flies captured at Smithsburg and pronounced them to be Photinus pyralis. Among these specimens there were some which were much smaller than others of the same sex, and I was of the opinion that they represented a different species. Dr. Chittenden, however, concluded

At that time the insects were very abundant. Dozens of them could be seen at a time flying about over the lawn and garden every evening. I do not know how early in the spring flight begins but after the first of August there were only very few seen, usually not more than two or three each evening. In October some were still seen. They probably continue to appear until prevented by frost.

The two sexes in the species studied are nearly alike. There is ordinarily but little difference in size, and the wings of the female, contrary to what is found in many species, are apparently as fully developed as are those of the male. The eyes, however, are much larger in the male than in the female and the luminous area is also much larger. In the male it covers the entire ventral surface of the three posterior segments, in the female only a portion of the ventral surface of the third. Thus, while the two sexes are similar in general appearances, they can readily be distinguished from each other.

HABITS

During the day time these fire-flies are found in dark crevices or under ground. In the evening when it is still light enough to read readily they come out. The males soon take wing and fly about, glowing fairly regularly at intervals of about five seconds. Owing to lack of proper instruments I was unable to ascertain the intervals very accurately. However, I found none less than four or more than six seconds. The females climb to the tips of blades of grass or onto other objects and usually remain quiet; they do not fly. Among all of the specimens captured on the wing during the entire season not a single female was found. My notes contain a record of sixty-one specimens taken

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that the small ones were dwarfs and that all are of the same species and identical with the fire-flies most common in Washington. If this identification is correct my studies were made on the same species as were those of Osten-Sacken and the major portion of those of McDermott. The reactions of the specimens found at Smithsburg, however, differ in at least two important respects from those of the specimens found at Washington judging from McDermott's description. He maintains (1) that the glow of the female is clearly of longer duration than that of the male; and (2) that there is an interval of nearly five seconds between the glow of the male and that of the female in response to it. I was unable to distinguish any difference in the duration of the glow in the two sexes at Smithsburg, and the interval between the glows is very little if any over one second. It seems quite remarkable that individuals of the same species should differ so much in their response, especially when there is so little difference in their environment as is found between Washington and Western Maryland.

thus, and there were probably fully as many more captured on the wing of which no record was kept. The wings of the females are, however, as previously stated, fully developed and they appear to have no difficulty in flying.

The males usually start to glow about ten minutes earlier in the evening than the females. The average time of the first glow for seven different days, not successive, between July 12th and 30th was 7:40½ P. M. for the males and 7:51 P. M. for the females. The time of the day the first glow appeared was surprisingly constant throughout the season. It was recorded on eighteen days between July 4th and 31st and on nine of these days it appeared between 7:35 and 7:40 P. M. Throughout the entire time the variation was only from 7:35 to 8 P. M.

I have no evidence indicating that the fire-flies, as might be expected appear earlier on dark, cloudy and rainy days than on bright, clear days. Low temperature, however, seems to retard their appearance. Specimens kept in darkness or in low light intensity during the day did not become active earlier than those under normal conditions. Males in darkness were never seen to glow spontaneously during the day, although the females were found to respond to artificial flashes of light at all times, and on one occasion after several responses of females to artificial light, a male nearby became slightly luminous and then ran about in an apparently excited manner and glowed a few times.

From the time the first flash of light for the evening is seen in the open the number of glows gradually increases until a maximum is reached between 8:30 and 9 P. M., after which there is a rather rapid decrease. Comparatively few flashes were seen after 9:30 P. M. and only rarely one after 11, although occasionally one was seen after midnight.

Thus it appears that the activity of these creatures is a periodic phenomenon to a considerable extent independent of immediate environmental changes.

REACTIONS

The male insects fly about in a leisurely sort of way, generally from one to two meters above the ground and glow as previously stated, at fairly regular intervals of approximately

five seconds. The relatively long abdomen hangs down nearly vertically, with the posterior end turned slightly up, so as to fully expose the luminous tissue to creatures below. The females, on the other hand, ordinarily remain quiet and do not glow unless they are stimulated. If a male glows within a radius of five or six meters of a female she usually responds almost immediately[3] by producing a flash of light. The male then turns directly toward her in his course and soon glows again. Following this the female again responds by glowing and the male again apparently takes his bearing, turns and directs his course toward her. This is repeated usually not more than two or three times before he gets near her and lights. Then he runs about in an apparently excited manner, glowing at irregular intervals, but orienting after each response of the female and proceeding toward her until his antennae come in contact with her, after which copulation takes place at once and all luminescence ceases. It is a very simple matter to follow a series of responses like this ending in copulation. The whole process as described was seen in very many different cases. There cannot be the slightest doubt as to the significance of the production of light in the creature studied.

If there is no wind the male usually lights within a few centimeters of the female, sometimes actually striking her. Thus they may come together in a very short time. But if it is windy the male frequently lights some distance from her and, especially if he becomes entangled in grass and other vegetation, as often happens, it may require many flashes of light, responses and reorientations and repeated flights before he actually finds her. After the male lights he apparently becomes much excited, as stated above, and usually runs about waving the antennae quite actively. The intervals between the flashes of light produced are much more irregular than when he is on the wing. During or immediately after each glow he stops, raises the antennae, takes an attitude of apparent attention and remains perfectly quiet until after the female answers with a flash, then he turns until he faces the direction in which the flash occurred

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[3] McDermott says (1911, p. 400): " The answering of the female does not occur immediately after the flash of the male, but at a period—apparently approximately constant for all females of this species—of about three to four seconds after the flash of the male. This slight delay occurred in every normal case of mating observed with this species, pyralis."

and proceeds. If the female does not respond, as frequently happens, he retains the attitude of attention for approximately a second and then continues on his course without turning.

The female glows in response to artificial light as well as to the glow of the male. In fact the response is apparently independent of the character of the light. I was able to induce it by flashes of light produced by means of an electric pocket lamp, parlor matches, tallow candles, kerosene lamps, sun light, light reflected from objects of various kinds, light passed through a plate of ruby glass or through a solution of copper sulfate. It is, however, dependent upon the duration of the illumination. The female will respond by glowing only if the light is turned on, left a certain length of time (a fraction of a second) and then turned off. She will not glow if it is not turned off after the proper exposure. This response is then clearly not due to light in itself but to changes in the intensity of the light. But it is equally clear that the essential factor in the response of the female is not changes of intensity but what such changes of intensity ordinarily represent, that is, the male.

A number of the characteristics in the behavior of the fireflies described above, as well as others are clearly brought out in the following quotation from my note book: On July 8 a female was caught at 8:15 P. M. and placed on the end of a pencil. Here she remained for fifteen minutes, almost perfectly quiet, while I moved the pencil about freely in studying the orienting reactions of several males on a sheet of paper. She was then taken to the porch, where I sat a short distance from the railing holding the pencil in my hand. I watched her carefully until 9:15, that is, for forty-five minutes. During this whole time she retained the same position and glowed only in response to flashes of light produced by males which occasionally chanced to fly near. The farthest distance of a male to which she responded was six meters. After I had been on the porch twenty minutes a male, attracted by the glow of the female, flew in and lit on the railing. Here he crawled about for nearly twenty-five minutes, glowing periodically at irregular intervals. One series of successive intervals recorded in seconds reads as follows: 35, 8, 12, 16, 5. The male turned toward the female every time she glowed in response to his illuminations, which was about two out of three times, but he could not get

to her without either flying or crawling down to the floor and then up on my leg. He did neither and consequently did not find her, although he was still active when the observations closed at 9:15. At that time the pencil containing the female was stuck into a crack in the wall at the back of the porch, about six feet from the floor, and left. At 2:20 A. M., the following morning, a male was found copulating with her. At 5:15 the male had left but the female was still on the pencil and had not moved. At 6 she was still there but at 7 she had disappeared.

FUNCTION OF LUMINESCENCE

Our description of the behavior of fire-flies demonstrates conclusively that luminescence functions in bringing opposite sexes together for the purpose of copulation. The following experiments show that this is the only factor involved in the phenomenon, that vision and smell play no part in it.

If a female is placed on the end of a pencil or small twig she remains quiet, as stated above, sometimes for many minutes and thus she can be readily transferred to any point desired. In studying the orienting reactions of the males on a sheet of paper I frequently made use of this method in handling the female. Under such conditions both respond normally and if not disturbed they soon come together, and copulate.

In these experiments I repeatedly held the female near the male and found that if she did not glow there was no indication of any response unless his antennae actually came in contact with her. Thus I have often seen a male, in running about, come within a centimeter of a female without the slightest appreciable change in his course and then after continuing several centimeters, sometimes twenty or more, turn about in response to her glow and proceed directly toward her. Sometimes, however, the males were seen to turn toward the female when they came near her; but I found that they turned toward the pencil quite as often when it did not contain a female. Consequently, while the turning of the male in these cases is evidently due to the presence of an object it is clear that he does not recognize the female by vision and that images of objects, if such are actually formed, play a very insignificant part in the process of mating.

In some insects mating appears to be controlled very largely

by chemical diffusion from the female. Mayer (1900) found this to be true for certain butterflies. The observations described above show that if diffusion of chemicals functions in the mating of the fire-flies studied, the chemicals must be emitted only in connection with the production of light. But that chemicals which may be thus emitted are insignificant in the process of mating is shown by the fact that if the females are enclosed in air-tight glass jars as was repeatedly done, the male finds them quite as readily as when they are free. (See experiment described below.) It is consequently clear that aside from actual contact the flashes of light produced by the fire-flies are alone functional in directing the male to the female in mating.

However, as previously pointed out for the female, so also for the male the responses preliminary to copulation are not primarily due to the effect of light in itself or to the effect of changes in the intensity of light. The responses are clearly given with reference to something which the flashes of light represent, a sexual phenomenon, preservation of the race, etc. Thus the fire-fly, although probably not conscious, acts with reference to the future. It may be said to project its present into the future, to live in the future as well as in the past and the present.

RECOGNITION OF THE FEMALE GLOW BY THE MALE

In many species the illumination produced by the male differs markedly from that produced by the female. In some the glow of the male is much more intense than that of the female. In others there is a marked difference in the duration of the glow of the two sexes. In still others the illumination has certain peculiar distinguishing characteristics, as, e.g., in Photinus sanguineus in which the male glow consists of two flashes of light separated by a short interval, while in the female it consists of but a single flash. In the Western Maryland species [4] I was unable to distinguish between the glow of the two sexes either in the quality or in the intensity of the light or in the duration or the nature of the glow. At times it did, indeed,

[4] McDermott (1911, p. 400) referring to Photinus pyralis says: "The flash of the female, while of the same colour as that of the male, is easily recognized after a little practice, being slower—or rather of longer duration—and less intense."

appear as though the males produced more intense flashes than the females, but if several of each sex were put into different glass jars, placed side by side and observed from a distance of two or three meters, as was repeatedly done, I was never able, by focusing attention on the character and the amount of light alone to distinguish one from the other with any degree of certainty.

The male fire-flies, however, seldom if ever respond to the glow of other males. In some way they appear to be able to distinguish between the flashes of light produced by the two sexes, as the following experimental observations clearly indicate.

A number of males were put into one glass liter jar and three females into another. Both were sealed and set in the garden 50 cm. apart. Thirty minutes later six free males had collected about the jar containing the females and none around the other jar. The two jars were then interchanged in position. Ten minutes later all of the males had again collected about the jar containing the females. These experiments were repeated with slight modifications on nine different evenings and the results in all cases were essentially like those stated above. Moreover, if a female and several males are put on a plane surface and closely watched, as was repeatedly done, the males seldom if ever make the mistake of turning toward other males. And again that the males recognize the glow of the females is clearly shown by the difference in the effect produced upon them by the glow of the two sexes as shown in the following experiment.

Five males were put into each of two glass liter jars labeled A and B respectively. The jars were then sealed and placed 50 cm. apart on a sheet of paper spread out on the ground. Four females were put into a 50 cc. bottle and placed 50 cm. from each of the two jars. Two free males soon came and lit on the paper. An opaque screen was then so arranged that the glow of the females could be seen by the males in one jar (A) but not by those in the other jar (B). The males in jar (A) and the two free males soon glowed freely, as did also the females. In fact they glowed so freely that there was almost a continuous flashing. The males in jar (B), however, presented a very different spectacle. They were watched carefully for fifteen minutes and during this time produced a total of only three flashes. It should be emphasised here that these males could

see the numerous flashes given by the males in the other jar but that they could not see those of the females. The screen was then removed so as to expose the females and it was found that the behavior of the males in jar (B) changed almost immediately. They became much more active and gave every appearance of being much excited; and in three minutes they produced a total of twenty-eight flashes of light as against three in fifteen minutes before the females were exposed. Such a specific stimulation of the male by the glow of the female is very evident to anyone making observations on these creatures and cannot be mistaken. It was observed again and again throughout the season under many different circumstances. A specific effect of the glow of the female is also attested by the fact that I was unable to induce the mating responses in the male by artificial imitation of the flashes of light produced by the females. Many attempts were made mainly with an electric pocket lamp but in only two or three instances was there any response on the part of the males used in the experiments, and in these it was not at all definite, although in practically all cases they responded definitely to the glows of females. ·

There are several factors that may possibly be involved in this phenomenon of recognition. Let us enumerate them: (1) The female is always at rest when she glows while the male is ordinarily on the wing; (2) the form of the luminous area differs in the two sexes; (3) there is always a certain time relation between the glow of the male and that of the female in response to it; (4) the quality of light produced by the two sexes may differ; (5) the intensity may differ; (6) the duration of the glow may differ.

Many observations and experiments were made in attempting to ascertain which of these factors are of importance in the process in question. I shall first describe the results of some of these and then attempt to interpret them.

(a) The mating responses are quite as precise when both male and female are at rest as they are when the male is on the wing, and the males are no more likely to turn toward other males. It is therefore evident that the fact that the female is at rest while the male is usually in motion when they glow can be of no particular value in the phenomenon of recognition.

(b) At different times, as previously stated, a piece of ruby

glass was held between male and female fire-flies so as to change the color of the light flashed from one to the other. This change produced no apparent effect on the mating responses of either. The female answered the male as promptly and the male turned toward the female as precisely as they did under normal conditions. The same was found to be true when the ruby glass plate was replaced by a flat flask filled with copper sulfate, or with a cylindrical bottle filled with water, or with one, two, three, or four thicknesses of paraffin tissue paper used in wrapping baker's goods.

These results seem to show that the recognition of the female by the male may be independent of any possible difference in the quality or in the intensity of the light produced by the two sexes, or of any possible difference in the form of the luminous area. Moreover the fact that males respond to females at various distances indicates that intensity cannot be of any special importance in this, and the fact that males hidden from females were often seen to turn toward glass jars or white paper from which the light produced by the females was reflected indicates the same with reference to form. We have left then as possible distinguishing characteristics seized upon by the male in the process in question, the time relation between the glow of the male and the response of the female and possible difference in the duration of the glow in the two sexes.

(c) Thirteen males were put into one glass liter jar and three females into another. These jars were then sealed and placed 25 cm. apart on a sheet of paper spread out in an open place in the garden. Ten minutes later three free males had collected about the jar containing the females and none around the other jar, although the thirteen males produced many more flashes of light than the three females.

One of the free males was captured and so oriented on the sheet of paper that he proceeded toward point very nearly midway between the two jars. He was rather sluggish and moved along slowly without glowing. When he reached a point nearly between the jars one of the males in the jar glowed. This did not appear to affect him in the least for he continued on his course without any apparent change until a female in the other jar answered the glow of the male, then he suddenly turned almost at once directly toward the female and imme-

diately became more active and apparently considerably excited. Shortly after turning he emitted a flash of light but he did not stop while he glowed as is ordinarily the case when the males are not on the wing. Similar reactions were seen many times in experiments made for other purposes so that there can be no question as to the accuracy of these observations. Moreover this experiment was repeated several times with different individuals and essentially the same responses were obtained in all.

In a few instances a free male turned toward the glow of a male in the jar, but the response was always much slower and less definite than an orienting response to a female, and invariably, if a female glowed after he had started toward the jar containing the males he turned about at once and proceeded toward her, whereas there was never the slightest indication of such a response to a male glow after he had once become directed toward a female.

These observations, especially the fact that the male, without having glowed at all, sometimes turns at once with scarcely any interval, toward the flash of light produced by the female, seems to indicate quite conclusively that the relation in time between the glow of the two sexes, that is, the fact that the glow of the female usually follows that of the male at a given interval, is not of prime importance in the recognition of the female by the male.

Thus we have excluded all characteristic differences between the response of the two sexes which might serve the male in distinguishing between them in the mating reactions save possible difference in the duration of the glow. But as was formerly stated no difference in duration could be definitely established. If the male, then, finds the female owing to unequal duration in the glow of the two sexes, as is probable, he must be so adjusted that he can detect differences too minute to be readily distinguished by the human eye.

ORIENTATION

The luminous or photogenic tissue in the female as previously stated is confined to a small area on the ventral surface of the third segment from the posterior end. Just before the female glows in response to a flash of light produced by a male she raises and twists the abdomen so as to direct the ventral sur-

face, the source of light, toward the male. If the male is directly above she twists the abdomen nearly through 180 degrees, if to the right or left through 90 degrees, etc. Only when the male is directly below does the female glow without first twisting the abdomen. These responses occur, in the Western Maryland species, almost invariably and they are so striking that they cannot readily be overlooked.

In thus directing the luminous surface of the abdomen toward the male no matter where he is located, it is evident that the character of the response must depend upon the location of the stimulus. It is markedly different when the light produced by the male strikes the anterior surface of the eyes than when it strikes the posterior or any other surface. To put it anthropomorphically, the female acts as though she recognized the spacial position of the male. In these responses the female does not begin to twist the abdomen until some little time after the male glows. Her reaction takes place in the total absence of the stimulating agent. After the flash of light which induced the response has vanished she directs the ventral surface of the abdomen toward the place where it was. It is therefore evident that the process of orientation in the female, (a response resulting in a position of the abdomen bearing a specific relation to the location of the male), is not regulated by the continuous action of the stimulating agent as is demanded by Loeb's theories of orientation (tropisms). The reaction is clearly due to change in light intensity; but it is without meaning unless it is referred to what the changes which induce the response represent, that is, the male and all subsequent occurrences in the process of reproduction.

In the male we find responses very much like those just described. The female produces a flash of light in answer to the glow of a male; then after a short interval, he turns, no matter what his axial position may be, until he is directed toward her and then proceeds. Thus if before the reaction he chances to be directed from the female he turns through 180 degrees, if at right angles to her through 90 degrees, etc. If the female is suddenly removed after she glows the response of the male is precisely the same. He turns through the proper angle and proceeds toward the spot where the female was when she glowed.

The accuracy of orientation in these reactions is really surprising. In making observations with reference to this point the female was usually put into a glass vial 2 cm. in diameter. This was set over a circle of equal size on a sheet of paper spread out on the ground. Males flying about were ordinarily soon attracted by the female and lit on the paper, sometimes very near the vial or on it, at other times 30 to 40 cm. away. In orienting after they lit they seldom failed to become directed toward a point within the circle under the vial no matter whether the female was removed immediately after she glowed or whether she was not removed at all.

The male usually does not begin to turn toward the female in response to her glow until the illumination has entirely disappeared. Thus, in the total absence of the flash of light which caused the reaction he turns through the proper angle, that is, he orients and proceeds toward the spot where the flash occurred. How is this possible? Does it mean that the male fire-fly can locate objects in space, that he has a spacial sense, that he knows and remembers the extent of turning necessary in order to direct his longitudinal axis toward any given point in space?

If we assume, just as in the case of the female, that there is in the male a specific response for the illumination of every surface of the eye; that is, that momentary illumination of the posterior surface is followed by turning through 180 degrees and then locomotion straight forward, the side of the eye by turning through 90 degrees and then forward movement, the front of the eye by forward movement alone, etc. It is not difficult to conceive all of these reactions to be purely mechanical, reactions of the nature of unconscious reflexes.

Whether or not the production of light in these insects is a sort of by product of metabolic changes, as maintained by many, it is evident that it is of fundamental biological significance. Indeed it is safe to say that its elimination would result in the destruction of the race and yet the light in itself can be of no special importance. The essence in the response of the male, like that in the response of the female, is not light but what light represents, that is, an individual of the opposite sex.

Males were at different times exposed in continuous illumi-

nation produced by means of a pocket electric lamp, a candle or a kerosene lamp. Only in two or three instances was there any indication of orientation and in these exceptional cases the reactions were very indefinite. These results, together with the fact that orientation in the male ordinarily does not begin until after the flash of light which induces it has vanished, demonstrate conclusively that the process of orientation and the direction of locomotion after orientation are not regulated by the continuous action of light, and that these reactions are consequently not in accord with Loeb's theories of tropisms according to which orientation is, as he puts it (1906, p. 135) "a function of the constant intensity." Stimulation which results in orientation in the fire-flies studied is unquestionably due to changes in light intensity much as it is in Stentor, Euglena and many other similar organisms (see Mast, 1911, pp. 80–205) and the insects remain oriented, not because of continuous action of light in accord with Loeb's theories, but because they tend to take a comparatively straight course in the absence of external stimulation. And since the external stimulating agent does not act continuously in directing this animal on its course after orientation, there can be no *a priori* necessity for assuming that it does in other animals, as Loeb (1911, p. 478), Parker (1912, p. 463) and others appear to hold.

The responses to flashes of light in both the male and the female fire-flies are unquestionably adaptive and an explanation for them must be sought along the same lines as an explanation for any other adaptive characteristic in living organisms. It is needless to add that the aim of practically all scientists in explaining natural phenomena, including the psychic, is to trace the order of events back to a mechanical basis. But we may as well face the facts squarely and realize that with reference to reactions it is questionable whether this has as yet been accomplished in even a single case. The assumptions of Loeb and Bohn to the contrary notwithstanding.

SUMMARY

1. The Western Maryland fire-flies are found in dark crevices or under ground during the day. In the evening, when it is still light enough to read, they come out; the females climb to the tips of grass or onto other objects and remain quiet; the

males fly about and glow fairly regularly at intervals of about five seconds. The females do not glow unless light from the males or from some other source is flashed on them.

2. Immediately before a female glows in response to a male she raises and twists the abdomen, until the luminous area on the ventral surface is directed toward him, no matter where he is located, then he ordinarily turns directly toward her and proceeds. These reactions are repeated until the two come together, after which copulation takes place at once. There is no other factor involved in mating. If a female is held near a male he pays no attention to her unless there is actual contact, showing that neither vision nor smell is functional in mating.

3. The males very rarely respond to the glow of other males or to flashes of artificial light. In some way they are able to distinguish between the illumination produced by the two sexes. Although no marked difference, either in quality or quantity, between the male and the female glow, was detected, experimental results indicate that there is probably a slight difference in duration and that this is the factor primarily involved in the phenomenon in question.

4. The males do not orient when exposed to continuous illumination. They respond only to flashes of light and the reaction does not begin until after the light has disappeared. Removal of the female immediately after she glows has no effect on this reaction. Thus orientation may take place in total darkness, and it is surprising how accurately these animals turn through the proper angle in the total absence of the stimulating agent that caused the response. Here we have a case in which it is clearly demonstrated that light does not act continuously in the process of orientation as demanded by Loeb's theories, a case in which it is also clearly demonstrated that continuous action of the stimulating agent is not necessary to keep the organisms oriented.

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OBSERVATIONS ON DOVES LEARNING TO DRINK

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The method of learning to drink has been studied carefully in fowls[1] and in a few other birds whose drinking resembles that of fowls.[2] But the drinking of pigeons differs from that of fowls in two important respects as follows: (1) Fowls and most birds drink by taking a little water in the mouth, then throwing the head up and swallowing this water, then lowering the head to refill the mouth, and so on. In contrast to this, all the pigeons (Columbidae), when they drink, hold the beak submerged in the water and gulp the liquid continuously. When it has finished and withdrawn the bill, the pigeon usually stands still, mumbling the bill a little and swallowing in a manner adapted to drain the throat and mouth; but even this part of the process has little resemblance to the drinking of fowls, for it is a very slight activity and the head is not raised above the normal. (2) The chick is precocial and must learn to drink soon after hatching. The pigeon is altricial, it is supplied by its parents with moistened food. It need not learn to drink for two weeks or more (the time varying somewhat with the species) and even after this period its learning to drink may be slow and gradual.

The following observations were made on the blond ringdove, *Turtur risorius.*

OBSERVATIONS ON DOVE NO. 43

This dove was hatched on December 17, 1910. It was fed plentifully by the parents for about 24 days, after which the parents were unwilling to feed it. By that time it had learned to eat seed quite proficiently, but had had no opportunity to learn to drink. It was then taken away from the parents and brought up by hand. It ate much seed for itself, but in addition soft food was placed by hand in its mouth and water was given it by means of a medicine dropper. It was not offered water

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[1] Breed, Frederick S. The Development of Certain Instincts and Habits in Chicks. *Behavior Monographs*, No. 1, 1911. pp. 8–13 are on drinking.

[2] Morgan, C. Lloyd. Habit and Instinct. London, 1896. pp. 44–46.

in a dish until the 28th day, from which date its diary reads
as follows:

28*th day.*—It has had no water since last night, but has eaten
a good deal of seed, must be thirsty. I give it water in the dish
from which it is accustomed to eat seed. To attract its attention,
I take water up in spoon (slowly, so as not to frighten it) and
drop the water again and again into dish. Dove watches the
dropping water with indifference. I then put many seeds into
the water and await results. Dove goes to dish in its accus-
tomed manner and begins to peck at the seeds. Getting the tip
of its bill wet, it shows surprise, starts back and shakes head,
throwing the water off. Then pecks at seed again, with same
result, but the shock of surprise a little less sharp. This re-
peated a great number of times; also, the dove sat on the edge
of dish and then walked in the water; but it does not drink.
This evening it was given a little water from medicine dropper.

29*th day.*—I tried the experiment as before, with same results,
the dove withdrawing its bill with apparent displeasure when-
ever it touches the water. Yet it must be thirsty.

30*th day.*—To see if it will drink by imitating the old ones,
I place it near the cage of an adult pair who have had no water
since yesterday and who will drink out of a cup as soon as it is
offered to them. I place the young so that it will see the two
adults drinking directly before it, and can drink out of the
same cup if it wishes. Result: The young watches them. As
they lower their heads and drink, it pays no attention to
this operation; but as they raise their heads again, it begs from
them strenuously.

Immediately after this test, I test the young by itself. I
decide to use a deeper dish than on the 28th and 29th days;
the dish in which it wet its bill before was too shallow for the
bill to be wholly immersed, though deep enough for an adult
to drink out of it easily. The deeper dish of water being put
in, with some seeds in the water, the dove soon comes and picks
up a floating seed, withdrawing its bill quickly from the water
as before. Then it apparently tries to pick a seed from bottom
of dish—when bill thus became immersed, the swallowing reac-
tion was immediately set up, evidently in a very mechanical
manner, the neck being strongly decurved, the eye half closing,
the whole head and neck rigid, while the mouth gulped slowly,

the entire reaction giving the impression that the bird had lost consciousness, or felt, if any consciousness, a painful one.

Conclusion: The young pigeon does not learn to drink by imitating drinking as such. It drinks first by an involuntary reflex act of swallowing when the bill becomes accidentally submerged in water.

31st day.—This dove has had no water since its one drink yesterday. 12:30 to 1.00 P. M. I keep the dish of water in its cage, and watch. Dove does not recognize the water, though I drop seed after seed into the water. Finally, about 1 P. M., dove having moved away from dish, I move the dish close to it. Suddenly, I know not why, it thrust bill into water, and immediately the swallowing reaction was set up. After swallowing several gulps, it withdrew bill and stood in rigid erect attitude, making swallowing movements in a stiff, mechanical manner quite unlike that of the adult.

32nd day.—I offered it water today in same dish as formerly. I tried for about ten minutes to call its attention to this water, by dropping seeds in, by moving the dish in front of the dove, etc.,—but all failed to attract its attention. Then I took a pencil and thrust the point of it repeatedly into the water. The dove immediately noticed this and began to thrust its bill into the water as the pencil had been thrust in. After two or three such thrusts, the next thrust took its bill deep into the water and the swallowing reaction ensued.

33rd day.—1 P. M. I put water dish in, "peck" in it with pencil, and drop in seeds and gravel, and thus succeed, after a time, in drawing dove to the dish. It puts down its bill *beyond* the dish and tries to drink there! But soon (from getting toes wet?) puts bill into dish and drinks.

6 P. M. (Room lighted by incandescent electric lamp.) I offer water, again "pecking" into dish with lead pencil. This keeps stimulating dove's attention. After a time it comes, puts bill down just *outside* the dish and tries to drink. Then walks around dish. I keep drawing its attention by dropping seeds into the water. It seems to want to drink, but does not again really try—until it steps full into the water; then it quickly puts bill in and drinks, as if stimulated by wet feet.

34th day.—6:30 P. M. (Electric light.) I put in same dish of water. Dove seemed to pay no special attention to mere pre-

sence of dish. But when I "pecked" in dish with pencil, it showed keen attention and activity, came out of its nest and to the dish and immediately drank, beginning the drinking movements apparently before it quite reached the water.

35th day.—8 P. M. (Electric light.) I put in same dish of water. Bird immediately shows interest, comes out of nest, walks near the water, back and forth, but does not drink. I then begin tapping in water with pencil. This excites the bird. It makes a slight begging movement toward the fingers holding the pencil. Then it makes a slight drinking movement, outside the dish. But though I tap long with pencil, and move dish about, it does not drink. Then I drop seeds into dish. It gradually concentrates its attention, finally runs at a dash into the dish and puts bill down beyond the dish and tries to drink there. Failing there, it immediately puts bill into dish and drinks a long, deep draft. What caused it thus suddenly to find the water? It may have been wet feet; or it may have been sight (reflection of the electric light?).

36th day.—2:30 P. M. I put in same dish of water. This time dove needs no tapping with pencil, no dropping of seeds. It soon concentrates attention, goes to dish, stops a moment, walks into dish and tries to drink from beyond it. Failing in that, it immediately puts bill into dish and drinks.

37th day.—10 A. M. Same dish put in. Bird recognizes it at once, walks into the dish, puts bill down beyond dish and tries to drink; seems disappointed and tries thus several times. Then walks beyond dish on floor, walks round to original side of dish, stops, and after a little hesitation and apparent "thought," puts bill down toward water, then into water, and drinks.

8:20 P. M. As I poured water into dish, out of sight of bird, it showed indubitably that it recognized the sound, trying to get out of cage toward source of sound, making slight movements which show thirst. On some previous days I have been quite sure that it did not recognize the sound of dropping water. I put dish in cage. Bird, in nest at other end of cage, reaches out vaguely toward dish, then bends down and tries to drink! This it repeats several times. It then comes down from edge of nest, walks toward dish, tries to drink outside dish, steps into dish, tries again without getting bill into water, soon steps

out of dish, and then appears as if not knowing what to do. After a minute or two, turning round, it goes to dish and with little hesitation drinks. Its success now seems due partly to accident, partly to abatement of its excitement.

38th day.—9 A. M. I put in same dish. Dove is a little frightened, but soon recovers, then goes straight to dish and drinks. Apparently it finds the water more easily by daylight and when wide awake than by lamp light and when not so wide awake. But even now, it drinks from extreme edge of water, at one end, as if its aim were at the dish, not the water.

39th day.—This forenoon I put water in cage in a dish of different shape from the customary one, and of glass, whereas the former one was of china. The dove came and drank from it almost immediately. However, I judge that this was chiefly because my hand putting the dish in gave it the cue. To test this, in the afternoon, I put in a tin cup full of water, contriving to keep the bird's attention elsewhere while I put it in. Result: The bird examined the tin cup a good deal, just as it would any strange object, but made no attempt to drink from it. Later I replaced the tin cup by a low tin dish. The two were in the cage altogether for an hour or more; they presented the further advantage that one was new and bright, the other tarnished, dark. Yet the bird tried neither of them. Then I took out the tin dish and put in the usual white dish: the bird drank from it after a few seconds' examination.

55th day.—After twenty-five days' experience, I believe this bird still does not recognize water as such.

Whenever the dish is put in, the bird at once puts its head down to drink, though it may not be near the dish; but it comes very soon to the dish and drinks readily from it.

OTHER OBSERVATIONS

Dove No. 46, hatched April 17, 1911, was similarly reared by hand. The history of its learning to drink, which was not recorded in detail, was much like that of No. 43.

In case of birds that have water in the cage all the time it is difficult to say when the young takes it first drink. Dove No. 22 was first observed to drink on the 22nd day. Such birds probably learn to drink more quickly than the subjects of the experiment, which saw water for only a short time each day.

A very young bird, even a nestling, will swallow copiously if it is taken in the hand and held with the bill submerged in water.

CONCLUSIONS

(1) The innate drinking activity of pigeons consists of bending the head down low and swallowing.

(2) The drinking reflex probably has no innate afferent inlet [3] except that of the touch of water on the inside of the mouth. The dove does not instinctively give a drinking response to the sight or sound of water, nor to the touch of water on distal parts of the body. The drawing back when the tip of the bill touches the water is especially interesting. The young dove first gets its bill into water, probably, chiefly by pecking; either pecking at objects in the water which attract its attention, or pecking in imitation of old birds.

(3) It is true that the young dove sometimes made a sudden response apparently to a beam of light on the water or to the touch of water on the feet. But these stimuli were not always effective; when they were effective, I judge that it was merely by catching the bird's attention. Pigeons, like jackdaws and bower-birds, are accustomed to peck at glistening objects.

(4) Though doves instinctively imitate pecking, they do not instinctively imitate drinking as such.

(5) The dove which was studied in most detail, dove No. 43, in drinking the second time (31st day) and the third time (32nd day) showed no evidence of remembering the first experience (30th day). But the fourth time (33rd day), and in all instances thereafter, it showed clear evidence of memory.

(6) In the course of experience the dove may associate the drinking reflex with all sorts of stimuli. Nos. 43 and 46 both associated it especially with the dish in which water was given and with the person who brought the dish. Even after much experience the dove may not recognize water as such.

(7) Doves which had imperfectly formed drinking associations frequently anticipated the reward of their efforts by making drinking movements before going to the water. This throws an interesting light on the purposiveness of animal behavior, and I hope to refer to it in another article.

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[3] This term I take from McDougall, William. An Introduction to Social Psychology. Boston, 1909.

(8) Is there any difference between fowls and pigeons in the respective parts played by instinct and by experience in drinking? We have not sufficient data, especially on pigeons, to answer this question. It would be well to investigate also the drinking of those birds of arid regions of which it is said that they never drink from pools of water but only from hanging drops. Wilson[4] says this of our prairie-hen. Such birds appear to be the extreme opposite of pigeons.

[4] Wilson. Alexander and Bonaparte, C. L. *American Ornithology.* Article on "Pinnated Grouse." In the edition published in Edinburgh in 1831, this statement is in Vol. II, p. 330–331.

REACTIONS OF CHICKS TO OPTICAL STIMULI

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From the Harvard Psychological Laboratory

One figure

In the course of a previous study,[1] in which the rapidity of development, permanency, and interrelation of certain habits in barred Plymouth Rock chicks were tested, the problem suggested itself of determining more accurately the nature of some of the optical stimuli in response to which a chick is able to acquire a habit of reaction. In these earlier experiments the animals were tested in their ability to discriminate two simultaneously presented stimuli differing essentially in color, form, or size. Although certain conclusions as to the *what* of discrimination seemed quite safe, it was thought best to conduct a further investigation in this direction with greater refinement of method. The earlier tests seemed to yield positive results in the discrimination of color and size differences, and negative results in the tests on forms.

The problem, then, became that of determining more accurately whether or not the elements of form, size, and color may become the basis of discrimination for the chick. The work was undertaken and completed in the Harvard Psychological Laboratory under the guidance of Professor Robert M. Yerkes, who proposed the investigation and assisted throughout with invaluable suggestions.

APPARATUS

A perspective of the apparatus employed is shown in figure 1. For a complete description, including dimensions of parts, the reader is referred to an article by L. W. Cole in an earlier number of this journal.[2] Following Cole's description, we may consider the apparatus as composed of three boxes: (1) The hover box, O; (2) the illumination box, covered by the

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[1] Breed, F. S. The development of certain instincts and habits in chicks. *Behavior Monographs*, vol. 1, no. 1, 1911, p. 41 ff.

[2] Cole, L. W. The relation of strength of stimulus to rate of learning in the chick. *The Journal of Animal Behavior*, vol. 1, no. 2, 1911, p. 112 ff.
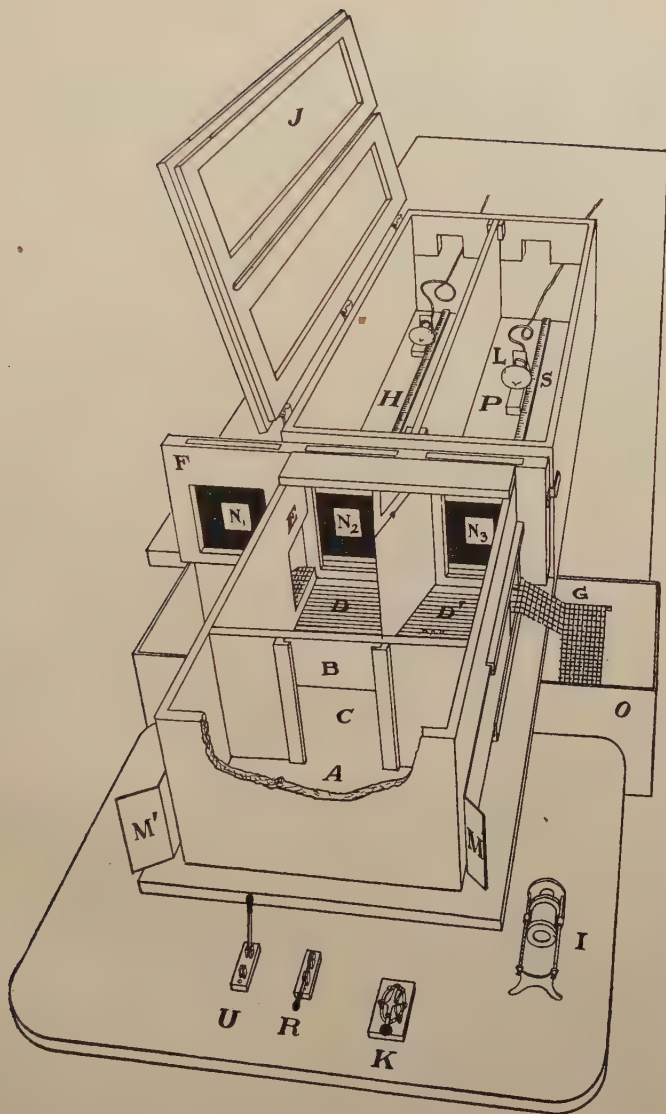
FIGURE 1. Perspective of apparatus used in testing reactions to colors, forms, and sizes.

1. *Hover box*, O; G, inclined planes of wire mesh leading from exits E, of the experiment box to the hover box.

2. *Illumination box.*—H, left compartment; P, right compartment; L, stimulus lamps; S, metric scales.

3. *Experiment box.*—A, entrance compartment; C, discrimination compartment; B, gateway between A and C; D and D′, electric passageways; N₁, N₂, N₃, glass areas for illumination in the sliding frame F; M and M′, cardboard shutters for closing exits E; U and R, electric keys for separate control of lamp in O and reading lamp (not represented in drawing) on outside of A, above R; K, stimulus key; I, inductorium.

The figure is symmetrical, hence the letters G, E, L, and S designate both the parts which they respectively mark and the duplicates of these parts on the opposite side of the figure.

lid J, containing the source lamps for the stimuli; and (3) the experiment box, divided into the two compartments, A and C. The illumination box and the experiment box were separated by a sliding frame F, containing three openings each 12 x 12 cm., in which were mounted the desired screens, N₁, N₂, N₃.

The point of the partition separating the electric passage-ways D and D′ was 31 cm. from the nearer ends of the metric scales.

In some respects a different adjustment of the apparatus from that used by Cole was employed by the writer. A 2 c. p. electric lamp instead of a 16 c. p. was located in the hover box. The inclined planes G, which Cole discarded, had been satisfactorily used throughout the present investigation. It may be more natural for a chicken to run up hill than down, as Cole intimates, but it is not quite so clear why the reader is asked, in explanation of the difficulty of descent, "to imagine a man descending a steep incline with his body leaning far forward." The difference in the results with this device is no doubt partly explained by the dark-room conditions maintained throughout the present test. The animals were attracted to the lamp in the hover box and did not wander off into the darkness after they reached it.

The source lamps in the illumination box were two turnip-shaped reflectors, having the lower half of the bulb frosted and the upper half mirrored. When operated at 110 volts, the end-on candle power, as measured at a distance of 3.048 meters, was 35.4 and 39.4 for no. 1 and no. 2, respectively, at the termination of the experiments. These measurements were made by the Electrical Testing Laboratories, 80th Street and East End Avenue, New York City.

The feet of the chicks were kept damp by a wet pad of cloth in the gateway B. This condition of the feet of the chicks insured greater regularity of the shock upon contact with the electric wires.

The experiments were all conducted in a dark-room. The apparatus within and without was painted a dull black. As a further precaution the discrimination compartment C, of the experiment box, was covered with a black cardboard hood so arranged that an opening above B was left of sufficient size to permit the experimenter to observe the behavior of an animal

in the presence of the stimuli. The black cardboard shutters M and M' were kept closed over the exits E until the animal had selected one or the other of the two stimuli. Thus the only light that reached a chick while in the act of discrimination was transmitted through the glass screens mounted in the sliding frame F. In the size and form experiments these screens consisted each of two plates of flashed opal glass, depolished toward the lamps, glossy-surfaced toward the chick. The illuminated areas of various sizes and shapes were produced by black mats of tin or cardboard that contained the appropriate openings and were set in the frame over the glass on the side away from the lamps. In the color work colored glass was inserted. The frame was adjusted on brass rollers that were constructed so as to work noiselessly. The lamps in the illumination box, mounted as they were on moveable cast-iron bases, could be shifted back and forth along the metric scales to provide such variation in the relative brightness of the stimuli as the demands of the experiment dictated.

The dark-basket mentioned in the following account was a willow basket lined with black cloth and covered with the same material. It was used for the purpose of dark-adapting the chicks. The animals were kept in this receptacle before and between trials during all the form and size work, and during all the color work except the preliminary tests.

METHOD

A chick that was being tested was introduced into the apparatus by hand at A, whence it passed through the gateway B, and walked toward one of the two lighted areas. If an error was made, the animal received an electric shock, controlled at K by the experimenter, whereupon it soon learned to pass to the other side of the compartment and secure its release. If a correct selection was made, the shutter M or M' was withdrawn, exit E was thereby slightly illuminated with the dim light reflected from the hover box, and the animal found its way down the inclined plane G to heat, food, light, and water. There was a possible source of error in the method at this point against which the operator had to take precaution constantly. He made it a rule not to withdraw the shutter until a chick was well onto the wires in a position to be shocked. Occasionally a chick would

stand near the edge of the electric wires and crane its neck toward the exit. It is easy to see how a slight noise on the proper side or a slight movement of the proper shutter might have precipitated a correct reaction when no discrimination of the important stimuli had taken place. The method was open to improvement at this point. So far as possible, chances for the involuntary interference of the experimenter should be eliminated. The writer was at work on an automatic device to meet this difficulty at the time these experiments were brought to a close.

The tests were given in series of ten trials each. In each series there was an equal distribution of the two stimuli on the right and left sides of the apparatus. These changes of position were handily produced by shifting the sliding frame, which contained like mounts at either end and the one to which these were opposed in the central opening. It is readily seen how a shift of the frame altered the relative positions of the two stimuli as well as changed the source lights for each.

The order of procedure was preference tests, training tests, and control tests. The first consisted of one or more series in which the chosen stimuli were alternated right and left and no electric shock was used. In the color work certain "preliminary" tests were made which were really of the nature of preference tests on various combinations of stimuli. In the training tests the right and left shifts were equally balanced but varied in order. In the control tests the shock was dispensed with.

REACTIONS TO COLORS

In the previous color tests, where the reflection method was used and black and blue were opposing colors, chicks not only formed the habit of rejecting blue but continued this rejecting reaction both when white was substituted for black and when a different tint of blue was substituted for that used in the original training. It seemed very probable that difference in color was the basis of discrimination. The experiment reported below was an attempt to test the color discrimination of the chicks by the transmission method. The colors chosen for this experiment were red and blue. During the course of the preliminary tests the following setting of the screens was adopted for the preference tests and the later training: Two red screens, one at either end

of the sliding frame, each composed of two plates of red glass cut from the same sheet; one blue screen, in the middle of the frame, made up of three plates of blue and violet glass. These color names represent simply what the colors appeared to the experimenter to be in advance of spectroscopic analysis. In each of the three screens the colored plates were covered on the side toward the chicks with a plate of opal glass, and over this was set a black mat with a circular opening 8 cm. in diameter. A spectroscopic analysis of the light transmitted by these screens was kindly made for the writer by Professors Yerkes and Cole, which showed the range of red to be from 760 to 640$\mu\mu$, and that of the blue-violet from 480 to 430$\mu\mu$.

That young chicks are positively phototropic was suggested by their crowding toward the light shortly after hatching in the incubator. The same tendency was indicated also by preliminary tests 4 and 5 (see table 1), in which no. 65 markedly preferred the brighter of two non-chromatic stimuli. When red and blue were approximately equal in brightness for the human eye, red was preferred by the chick. See preliminary tests 1–3. Even when red was considerably less bright than blue, as judged by the human standard, the chicks still selected red in preference to blue. After no. 65 had selected the dim red in series 6 in preference to the comparatively bright blue, series 8 and 9 were arranged to discover whether the animal was exhibiting either a negative reaction to blue or a positive reaction to darkness. The result showed clearly that neither of these possibilities obtained. Blue 10 was preferred to darkness, 9–1. But when the distance of the source light from the color screen was increased from 10 to 80 cm., the preference of the chick for blue as against darkness was only slightly evident. Again, when the stimuli were red 100 and blue 10, no. 58 and no. 65 each selected blue nine times, red once. When, with no. 58, blue was kept constant at this intensity and red was gradually increased in brightness to 40, the preference was as gradually shifted to red. A like result was found in the tests on no. 65 immediately following. Thus, while the chicks had a natural preference for the brighter of two non-chromatic stimuli, the same could not be said of chromatic stimuli as humanly estimated. The peculiar preference for red when opposed to blue of much greater brightness value pointed to

one or both of the following conclusions: (1) A difference exists
between the chromatic luminosity values for the chick and those
for the human; (2) chicks exhibit a qualitatively determined
preference, such as is apparent in some other animals. Since,
however, the preference of the chicks for red and blue varied
with the variations in the relative brightness of the two color
stimuli, brightness was clearly shown to be a controlling factor.
Whatever natural preference the chicks might have had for
red, this was overcome, in every case tried, by a sufficient rela-
tive increase in the intensity of the opposing blue. In view of
these facts it was thought best at this stage of the investigation
to seek such intensities of red and blue that initial preference
for neither would appear. This point of indifference once located,
it was planned to proceed with a process of training to deter-
mine the ability of the chicks to discriminate between two such
red and blue stimuli. In the final preliminary tests red, from
a source light 60 cm. distant from the screen, with a blue from
a source of about equal power, 10 cm. distant, gave the reaction
records of 6–4 and 7–3 for chicks no. 58 and no. 65. Red 70
with blue 10 resulted 4–5 and 3–7 for no. 61 and no. 65, re-
spectively. Hereupon, the apparatus was slightly modified in
preparation for the more careful preference tests that preceded
training on the indifferent combination such as red 70, blue 10
seemed to approach. Cardboards containing circular openings
8 cm. in diameter replaced those with rectangular openings
used in the preliminary tests. Circular water screens (Bausch
and Lomb projection-lantern cooling cells) 12.5 cm. in diameter
and 4.8 cm. thick were substituted for the rectangular cells in
use up to this time. Furthermore, during the preference tests
and throughout the following training and control tests, provi-
sion was made for the dark-adaptation of the animals by keep-
ing them in the dark-basket in the dark-room for a period of ten
minutes each day just prior to experimentation. Between trials
also each chick was kept in the dark-basket. Among the prefer-
ence tests, A–F, with red 70 opposed to blue 10, red was selected
by the four chicks 28 times, blue 52 times, out of a total of 80
trials. Red and blue at these intensities, although not ideally
balanced, were weighted on the proper side for a test of the
chicks' ability to form a habit of positive reaction to red, so

training to this end was begun. The habit proved a compara-
tively easy one for the chicks to form, as evidenced by the first
training series, 1–8. Each of the four animals finished the
training, including the final twenty perfect reactions, within a
total of 80 trials. When all the chicks had formed the red-
blue habit perfectly, a slightly different intensity of blue was
opposed to red at 10 and 100 alternately. The chicks con-
tinued the specific reaction to red, two of them without error.
They had evidently not formed a habit of specific reaction to
red or blue of a particular brightness value. As soon as the
original habit was ascertained to be in perfect condition in all
the chicks, they were tested further with red and blue, each color
this time being used equally often at the value of 10 against the
other color at 100 in a series of ten trials. Surprisingly, not a
single error was made in this series by any chick. It is well
to bear in mind that blue 10 was without question much brighter
than red 100; and red 10 than blue 100.

Elsewhere[3] the writer has said something about Yerkes' dis-
crimination method and the peculiar emphasis that sometimes
attaches to the stimulus in connection with which the electric
shock is administered. This emphasis on the blue was very
noticeable in the results from all four chicks. When white light
was opposed to blue in the control test, the chicks uniformly
rejected blue, regardless of which stimulus had the greater
brightness value. When white was substituted for blue and
the factor of brightness eliminated by variation, the score was
red 29, white 27, in a total of 56 trials. No. 61, however, with a
little training formed a perfect red-white habit, the element of
brightness being again eliminated in the manner just mentioned.

What shall be our interpretation of the above facts? When
the stimuli were red 70 versus blue 10 in the preference tests,
no marked preference was shown for either stimulus. Prefer-
ence shifted decidedly to blue in the combination red 100
versus blue 10, and just as decidedly to red in the combination
red 40 versus blue 10. That is, from the indifference point prefer-
ence varied as the relative brightness of the stimuli varied. It
seems reasonable to suppose, therefore, that at the above in-
difference values, the two stimuli were approximately equal in

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[3] *Loc. cit.*, p. 69.

brightness for the chicks, provided brightness alone was the determining factor in the preference. The readiness, however, with which the chicks came to discriminate these two stimuli leads one to suspect that the basis of the discrimination was not difference in brightness. But this result alone is not proof conclusive that color was a factor. A point of brightness indifference may not mean brightness equality, nor need brightness equality for the chick in advance of training mean brightness equality after training. The selective reaction might therefore have been based on difference in brightness. But the evidence that color was a factor in these reactions does not rest on the fact alone that the indifference stimuli were discriminated. The fact that blue of different brightness value from that used in the training was rejected consistently when appearing with red that was not the same in brightness as the original red, ruled out the probability of specific reaction to specific brightness values. And more important still was control test 5. When red was increased in brightness from 70 to 10 and the accompanying blue decreased from 10 to 100, blue was rejected. When red was decreased from 70 to 100 and used with blue 10, blue was again rejected. Alternations of these combinations failed to interrupt the specific rejection of blue. It should be borne in mind that red 10 was brighter than blue 100 both for the chick (see preference test C) and the human; and red 100 was less bright than blue 10 both for the chick (see preference test F) and the human. Finally, in the control test on white-blue, the rejection of blue continued perfectly when white was much brighter and when it was much less bright than blue. Thus it seems almost certain that the quality of the stimulus as well as quantity played a determining part in the reactions of these animals.

An attempt was made to photometer the stimuli with a Lummer-Brodhun photometer and a Hefner amyl acetate lamp, but without success, primarily on account of the very low intensities of the weaker stimuli. But even had the intensities of the colored lights been sufficiently high for examination by this method, limited progress would have been made toward an objective measurement of the color values, for this method depends upon a human judgment such as we have already given. Radiometry is the hope of the experimenter in this difficulty.

TABLE 1

RED-BLUE REACTIONS

Chicks hatched Oct. 26, 1908

Series	Date	No. 58 Sex, F. Red Blue		No. 61 Sex, M. Red Blue		No. 62 Sex, M. Red Blue		No. 65 Sex, M. Red Blue		Remarks
Preliminary Tests
1	Nov. 17			10	0	10	0			Both lamps at 40
2	" 18			10	0	9	1			Both lamps at 40
3	" 19					10	0			Both lamps at 40
								Btr.	Dkr.	
4	Nov. 18							8	2 ⎰	Lamps at 20 and 70, varied r
5	" 19							10	0 ⎱	and l. Opal glass.
								Red	Blue	
6	Nov. 20	10	0	10	0			10	0	Right lamp, 10; left, 80.
7	" 20					10	0			Right lamp, 20; left, 70.
								Dk.	Blue	
8	Nov. 24							1	9	Darkness; B, 10.
9	" 24							4	6	Darkness; B, 80.
								Red	Blue	
10	Nov. 25	1	9					1	9	R, 100; B, 10.
11	" 25	⎰0	6							R, 50–80; B, 10.
		⎱3	1							R, 40; B, 10.
12	" 25							⎰5	0	R, 40 and 50; B, 10.
								⎱2	3	R, 60; B, 10.
13	" 26	6	4					7	3	R, 60; B, 10.
14	" 26			4	5			3	7	R, 70; B, 10.
Preference Tests
A	Nov. 28	6	4	1	9	3	7	4	6	R, 70; B, 10.
B	" 30	5	5	1	9	3	7	5	5	R, 70; B, 10.
C	Dec. 1	9	1	1	9	9	1	9	1	R, 40; B, 10.
D	" 1	0	10	0	10	0	10	5	5	R, 100; B, 10.
E	" 2	10	0	3	7	8	2	9	1	R, 40; B, 10.
F	" 2	3	7	1	9	1	9	5	5	R, 100; B, 10.
Training Tests
1	Dec. 4	5	5	4	6	5	5	5	5	R, 70; B, 10. Sk, 6
2	" 5	5	5	8	2	7	3	6	4	R, 70; B, 10. Sk, 6.
3	" 7	9	1	7	3	6	4	7	3	R, 70; B, 10. Sk, 6.
4	" 8	9	1	8	2	6	4	9	1	R, 70; B, 10. Sk, 6.
5	" 9	10	0	8	2	10	0	10	0	R, 70; B, 10. Sk. 6.
6	" 10	10	0	8	2	8	2	10	0	R, 70; B, 10. Sk, 6.
7	" 11			10	0	10	0			R, 70; B, 10. Sk, 6.
8	" 12			10	0	10	0			R, 70; B, 10. Sk, 6.
Control Tests
1	Dec. 13	10	0	7	3	8	2	10	0	R, 10 & 100 alt.; B, 20.
2	" 14	9	1	10	0	10	0	10	0	R, 70; B, 10. Sk, 6.
3	" 14	9	1							R, 70 B, 10. Sk, 6.
4	" 14	10	0							R, 70; B, 10. Sk, 6.
5	" 15	10	0	10	0	10	0	10	0	R & B, 10 & 100, alternately.
6	" 16	8	2					9	0	R, 70; B, 10.
7	" 16			⎰8	0	6	4			R, 7–100; B, 7–105.
				⎱1						R, 100; Darkness.
					1					Darkness; B, 10.
8	" 17	6	0	6	0	5	1	6	0	R, 70; B, 10.
		White	Blue	White	Blue	White	Blue	White	Blue	
9	Dec. 17	10	0	10	0	10	0	10	0	B=, <. and > W in brightness
		Btr.	Dkr.	Btr.	Dkr.	Btr.	Dkr.	Btr.	Dkr.	
10	Dec. 18	2	6	8	0	6	2	5	3	Both sides W. Opal glass.
		Red	Blue	Red	Blue	Red	Blue	Red	Blue	
11	Dec. 21	4	0	4	0	4	0	4	0	R, 70; B, 10.

TABLE 1—*Continued*

Series	Date	No. 58 Sex, F. Red White		No. 61 Sex, M. Red White		No. 62 Sex, M. Red White		No. 65 Sex, M. Red White		Remarks
					Control Tests—*Continued*					
12	Dec. 21	8	6	10	4	4	10	7	7	R, btr. 6 trials; W, btr. 6; eq. 2.
13	Dec. 21	Red Blue 5 1		Red Blue 4 2		Red Blue 4 2		Red Blue 4 2		R and B varied in brightness, now one, now the other brighter, with extreme diff's.
14	Jan. 4	Red Blue 4 0		Red Blue 4 0		Red Blue 4 0		Red Blue 4 0		R, 70; B, 30.
15	Jan. 4	Red White 5 5		Red White 8 2		Red White 6 4		Red White 5 5		R, 6–30; W, 15–105.
					Training Tests					
1	Jan. 5			9	1	5	5			R, 6–30; W, 15–105.
2	" 6			8	2	9	1			R, 6–30; W, 15–105.
3	" 6			9	1	8	2			R, 6–30; W, 15–105.
4	" 7			10	0	9	1			R, 6–30; W, 15–105.
5	" 7			10	0	8	2			R, 6–70; W, 70–105.*
6	" 8					6	4			R, 6–70; W, 70–105.
7	" 8					7	3			R, 6–70; W, 70–105.
8	" 8					7	3			R, 6–70; W, 70–105.
9	" 9					8	2			R, 6–70; W, 70–105.
										Note: No. 62 large, slow, and inactive from start. At time of last test physically weak.

*R, 10 > W, 100 in brightness.

Explanation of abbreviations in table: R, red; B, blue; W, white; Sk, electric shock; Dk, darkness; Btr, brighter; Dkr, darker; Eq, equal.

A numerical value appearing with the name of the stimulus represents distance in centimeters of the source light from the screen.

REACTIONS TO FORMS

As a test of form discrimination chicks were afforded an opportunity to select a circle when appearing along with a square. For this experiment the sliding frame of the apparatus was fitted with three black tin plates, in two of which had been cut square openings each with a side of 4.43 cm.; in the third and central one was cut a circular opening of the same area, its diameter being 5 cm. Compactly behind each of the form plates were mounted two plates of opal glass, each pair of plates having an aggregate thickness of about .515 cm. The lamps were stationed at a distance of 90 cm. from the screen. The Bausch and Lomb projection-lantern water cells were adjusted immediately back of the opal glass plates, on the side of the source lights. With the above arrangement white lighted areas with sharp outlines were presented to the animals, with variations in brightness, size, and position under good control.

Three chicks, nos. 73, 76, and 87 were used in these tests, one of which yielded positive results. After 60 training tests,

no. 73 was unfitted for further work by a misuse of the electric shock. When no. 87 had completed 160 trials in the training, the work was discontinued on account of the poor physical condition of the animal. Starting with preference trials of 9 reactions to the circle and 11 to the square, its total number of reactions to the circle during the training was 101; to the square, 59. The final two series registered 9–1 and 8–2 in favor of the circle. There were thus indications that the training had been somewhat effective.

The results from no. 76, on the other hand, were more convincing. Reacting indifferently in the preference tests to the circle and the square of equal area and brightness, it was able to select the circle 38 times out of the last 40 trials in a training series of 120 trials. When the positions of the source lights were shifted from 90 to fixed positions at 80 and 100 cm. respectively, so that the forms were illuminated unequally, no. 76 selected the circle 18 times out of 20 trials. Training was then resumed for two series with the forms of equal brightness, after which the sliding screen was mounted from left to right as follows: 5 cm. circle, 4.43 cm. square, and a circle equal to that circumscribed about the 4.43 cm. square. Ten trials with this combination netted 8 selections of the circles and 2 of the square. When, however, the next change in the forms was made, there appeared to be no sign of discrimination. The corresponding inscribed circle was substituted for the circumscribed, accompanying as in the previous test the square and circle equal to each other in area, and the first ten reactions recorded were 5 for the circles and 5 for the square. An attempt was now made to train the chick to select these circles in preference to the square. After this training had been prolonged for 70 trials, the chick was selecting the circles as against the square 9–1. At this point the frame was set with the circumscribed and the inscribed circles in combination with the square, whereupon the chick made the record 10–0. For the series following this one, conditions remained the same except that the lamps were exchanged in the illumination boxes and a different tin plate was used to produce the square form. The series resulted 9–1. When this series was repeated with a different order of shifts of the frame, the animal made the record 10–0. For data see table 2.

TABLE 2
Circle-Square Reactions
Chick No. 76.   Sex, F.
Hatched December 3, 1908

Series	Date	Right	Wrong	Remarks
A	Jan. 21	4	6	Cir. and Sq. equal in area and brightness.
B	" 22	5	5	" " "
1	" 23	6	4	" " "
2	" 24	6	4	" " "
3	" 25	2	8	" " "
4	" 25	7	3	" " "
5	" 25	10	0	" " "
6	" 26	6	4	" " "
7	" 26	9	1	" " "
8	" 26	5	5	" " "
9	" 26	9	1	" " "
10	" 26	10	0	" " "
11	" 26	10	0	" " "
12	" 26	9	1	" " "

Control Tests

1	Jan. 27	9	1	Lamp, r, 80; lamp, l, 100.
2	" 27	9	1	Lamp, r, 100; lamp, l, 80.

Training Tests

13	Jan. 30	7	3	Cir. and Sq. equal in area and brightness.
14	" 30	9	1	" " "

Control Tests

3	Jan. 30	8	2	Sq. vs. equivalent and circumscribed circles.
4	" 30	5	5	Sq. vs. equivalent and inscribed circles.

Training Tests

15	Jan. 30	8	2	Sq. vs. equivalent and inscribed circles.
16	" 30	6	4	" "
17	" 30	7	3	" "
18	" 30	8	2	" "
19	" 30	9	1	" "
20	" 31	7	3	" "
21	" 31	9	1	" "

Control Tests

5	Jan. 31	10	0	Sq. vs. circumscribed and inscribed circles.
6	" 31	9	1	Same, lamps exchanged. New Sq. form plate.
7	" 31	10	0	Same, different order of stimuli.

After negative results in several experiments on forms, the results obtained with no. 76 are interesting.   I believe I was fortunate in the choice of animal for this work.   My notes

describe this chick as rather undersized, strong, active, sensitive, cautious, and quiet. Detailed records of its reactions show that selection of stimuli was made by affirmation and negation most frequently, by comparison occasionally.

REACTIONS TO SIZES

The method of testing size discrimination was similar to that followed in the tests on forms. Two circular areas of different size were presented to the chicks, one 5 cm. in diameter, the other 8 cm. In the sliding frame of the apparatus an 8 cm. circle was mounted at each end, a 5 cm. circle in the middle. In other respects the appointments of the apparatus were the same as in the form experiments.

In these tests three factors were taken into consideration, any one of which might have become a means of discrimination:

1. Difference in size of the lighted areas,
2. Difference in brightness of the lighted areas, and
3. Difference in brightness of the right and left sides of the experiment box.

To eliminate other means of discrimination but the difference in size of the lighted surfaces, the following list of tests was adhered to throughout the training:

1. Sides of box equal in brightness: S, 60, r; L, 96, 1
2. Sides of box equal in brightness: S, 60, 1; L, 96, r
3. Circles equal in brightness: S, 96, 1; L, 96, r
4. Circles equal in brightness: S, 96, r; L, 96, 1
5. Large circle the brighter: S, 80, 1; L, 40, r
6. Small circle the brighter: S, 40, r; L, 80, 1
7. Large circle much the brighter: S, 100, 1; L, 30, r
8. Small circle much the brighter: S, 30, r; L, 100, 1
9. Sides of box equal in brightness: S, 60, r; L, 96, 1
10. Circles equal in brightness: S, 96, 1; L, 96, r

Explanation of abbreviations: S, small circle; L, large circle; numbers, distances in centimeters of source lights from screen; r, right; 1, left.

The experiment was undertaken with chicks no. 70 and no. 83. The preference tests showed a marked inclination of the chicks to react positively to the larger or negatively to the smaller of the two circles, each animal reacting 8 times to L

and only 2 to S. The plan of the work was interfered with somewhat by the necessary retirement of no. 70. After 120 trials this animal was unable to continue on account of physical debility, an unfortunate failing of these laboratory chicks after a given period. No. 70, however, showed signs of acquiring the small-large habit, for in its last 50 trials there were 38 reactions to S and 12 to L. No. 83 remained in the experiment with the positive result shown in table 3, which follows:

TABLE 3

SMALL-LARGE REACTIONS

Chick No. 83.   Sex, M.

Hatched December 12, 1908

Series	Date	Right	Wrong
A	Jan. 13	2	8
1	" 14	2	8
2	" 15	3	7
3	" 16	5	5
4	" 18	5	5
5	" 19	6	4
6	" 20	3	7
7	" 21	7	3
8	" 22	8	2
9	" 23	5	4
10	" 24	5	5
11	" 25	6	4
12	" 27	4	6
13	" 27	7	3
14	" 27	5	5
15	" 27	6	4
16	" 27	9	1
17	" 27	6	4
18	" 28	8	2
19	" 28	8	2
20	" 28	9	1
21	" 28	8	2
22	" 28	10	0
23	" 28	10	0
24	" 28	10	0

SUMMARY AND CONCLUSIONS

The chicks in advance of training selected the brighter of two non-chromatic stimuli.

According to the human standard of brightness values, a similar law did not hold for chromatic stimuli. This exception points in the direction of one or both of the following conclusions:

(1) A difference exists between the chromatic luminosity values for the chick and those for the human;

(2) Chicks exhibit a qualitatively determined preference, such as is apparent in some other animals.

Brightness was found to be a controlling factor in the responses to optical stimuli.

All four chicks after brief training formed the habit of selecting without error one of two colors at the brightness-indifference point.

This selective reaction was not determined by red or blue of particular brightness values; neither was it determined by the relative brightness of the two stimuli.

Thus seemed verified a conclusion of our earlier work, namely, that quality as well as quantity of the optical stimulus played a determining part in the reactions of these animals.

Positive reaction to a given stimulus as indicated in a table of reactions did not necessarily imply specific reaction to that stimulus. It sometimes meant merely a specific rejection of the opposing stimulus.

A chick learned to discriminate two optical stimuli on the basis of difference in form.

A chick learned to discriminate two optical stimuli on the basis of difference in size.

NOTES

BEHAVIOR OF THE YOUNG BIRD IN BREAKING OUT OF THE EGG

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The older naturalists, especially Réaumur, made some careful observations on the behavior of chicks in breaking out of the egg. Their observations are summarized in one[1] of Rennie's excellent little books. The main facts are these. The chick chips the egg a little at a time with its bill, and as it does so it turns around inside the egg-shell, the axis of its rotation being precisely the long axis of the egg. The consequence of this turning is that the tip of the bill, chipping the shell as it goes, describes a very exact circle around the large end of the egg, and thus the large end of the shell is cut off. The time which it takes to finish the cutting is very variable. When the opening has been extended nearly or quite around the egg, the chick pushes in such a way as to separate the two sections of the shell and tear any shreds of membrane which may have been holding them together. Thus the little bird effects its escape.

From the fact that pigeons' eggs are invariably opened by a cut which neatly encircles the large end, we should infer that the young pigeon opens its egg in the same manner as does the young chick. And this conclusion is confirmed by the following observations on two young doves (Turtur risorius). The accounts are transcribed from my notes.

"No. 46, April 19, 1911. 8:30 A. M. My wife found egg chipped and called me to see it. While we watched it, the young chipped the egg about one-third the way round (120°) in about ten minutes. The young made a strong movement, then rested for several seconds, then made another strong movement, and

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[1] [Rennie, James. Published anonymously.] The Domestic Habits of Birds. London, Charles Knight, 1833.

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so on.[2] Each movement seemed to consist of (1) Pushing out the large end of the egg, i.e., pushing lengthwise of the egg; (2) thrusting the bill through the shell, the bill coming just far enough to break through, in fact many times not breaking through but only bulging the shell; (3) turning round a few degrees. We could see this turning through the hole in the shell; also we could see that each thrust of the bill appeared a little beyond the previous one. With the egg large end up, the turning was anti-clock-wise.

"Not wishing to sacrifice the life of this young bird, I replaced it in nest under parent. 9:45 A. M. We look and find young out of shell."

"No. 51, August 28, 1911. Just after 2 P. M., I put seed in the pen, and sitting bird comes off the nest to feed. I see that egg is chipped almost all the way round, and soon the young bird makes intense struggle to get out. It makes a strong effort, and then rests, breathing deeply and rapidly, about eight or ten seconds, then makes another strong effort. Once, apparently more exhausted than usual, it rested nearly forty seconds. After several such movements it got the halves of the shell separated at an angle (they still held together at one point). During the next few struggles it sometimes seized edge of shell with one foot and apparently tried to push it away. But the final dislodgment of shell seemed to be made by powerful movements of head and neck. I was surprised at the violence of the movements.

"Having got out, it rested on ventral surface. When touched, moved the head a little, but seemed unable to raise head from nest."

The question arises: By what means does the little bird turn around inside the egg-shell? When I asked Professor Whitman this question, he answered thus: "The bill itself may pull or push the embryo round in the egg. Yet I think the turning may be done by the feet. I think it would not need much force. I have taken an egg between my finger and thumb, just before hatching, and have felt a bumping inside; I feel very sure that this was not imagination. The bumping may have been caused by the bill, but more probably by the feet. The little fellow is

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[2] Similar rhythmic activity was noted by Breed in the chick. Breed, F. S. The Development of Certain Instincts and Habits in Chicks. *Behavior Monographs*, No. 1, Boston, 1911. See pp. 5–7.

undoubtedly in a very uncomfortable position, with the head pushed between one wing and leg, and this is what makes it move and thrust the bill against the shell of the egg. The opening and closing of the bill, which is seen in the young pigeon within the egg, is supposed to be due to gasping for air.'' To determine whether the chick turned itself round by its bill or by its feet, Réaumur tried the experiment of breaking away the shell in advance of the bird's bill, so that the bill had nothing to push against; "the consequence was, that each chick was sooner released from confinement than if it had had to effect its own exit." From which, Réaumur concluded that the turning was probably performed by means of the feet.[3]

This general method of breaking the shell, which we have seen to be common to the domestic fowl and pigeons, Réaumur found to hold also for ducks, and he thought it probable that it was common to all birds.[4] Observations of the hatching activity of wild forms are, naturally, rare.[5] The indications are, that the type of behavior which we have described is common to most if not all the Carinatae. But in the ostrich, although the posture of the young within the egg[6] much resembles that in the Carinatae, there are some considerations, one of which is the extremely hard egg-shell, which lead one to suspect that the mode of exit of the young ostrich must differ from that of the young carinate bird.

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[3] Quoted in Rennie. *Op. cit.*, pp. 167–168.

[4] Rennie. *Op. cit.*, p. 171.

[5] I have happened upon only two, each recorded all too briefly. Hudson, W. H. The Naturalist in La Plata. London, 1892. Page 112 records observed hatching of the Jacana. Moore, R. T. The Least Sandpiper During the Nesting Season in the Magdalen Islands. *The Auk*, Vol. 29, N. S., April, 1912. Page 218 records observed hatching of this Pisobia.

[6] Beebe, C. W. The Bird, its Form and Function. New York, 1906. See figs. 370 and 371.